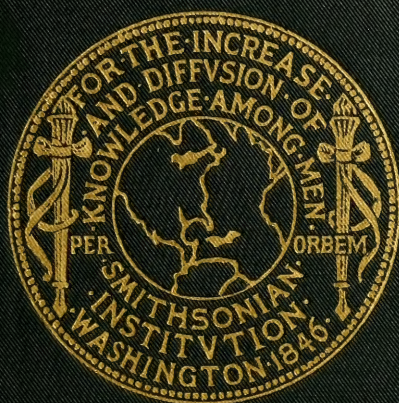








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SMITHSONIAN INSTITUTION  
UNITED STATES NATIONAL MUSEUM  
BULLETIN 169

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THE FORT UNION OF THE  
CRAZY MOUNTAIN FIELD, MONTANA  
AND ITS MAMMALIAN FAUNAS

BY  
GEORGE GAYLORD SIMPSON  
*American Museum of Natural History  
New York City*



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Dedicated to the Memory of

**James Williams Gidley, Ph. D.**

1866-1931

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The scientific publications of the National Museum include two series, known, respectively, as *Proceedings* and *Bulletin*.

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ALEXANDER WETMORE,  
*Assistant Secretary, Smithsonian Institution.*

WASHINGTON, D. C., *June 16, 1937.*

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# THE FORT UNION OF THE CRAZY MOUNTAIN FIELD, MONTANA, AND ITS MAMMALIAN FAUNAS

---

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## INTRODUCTION

THIS WORK is chiefly devoted to the description and discussion of a large collection of Paleocene mammals, from the Fort Union of central Montana, belonging to the United States National Museum. The first part of the memoir is geological, chiefly stratigraphic and paleontological. The location and general characteristics of the mammal-bearing area are described, followed by a résumé of its stratigraphy and geologic structure. The general areal geology is only briefly outlined, and details are largely confined to the beds in which the mammals occur. In the paleontological section, the various fossil localities are listed, and the mammalian fauna of each is given, together with a summary of all fossil mammals found in the field. Faunal succession and faunal correlation, supplementing the remarks made in the previous section on more purely stratigraphic correlation, are discussed in detail. The general aspect and ecologic relationships of the mammalian faunas are also discussed. Nonmammalian fossils are incidentally mentioned, without any attempt at exhaustive treatment.

The second and longer part of the memoir is zoological and is devoted to definitions of all taxonomic groups which were originally described from this field or the conception of which is markedly affected by material from here, to discussion of the relationships and phylogeny of the mammals represented, and to description of the specimens in the collection.

Geology outside the area of reference and mammals other than those definitely identified here are mentioned only for the sake of comparison.

In addition to the National Museum collection, specimens from this field now at Princeton University are included. Reference is also made to a small collection in the Carnegie Museum, but since this includes nothing not better represented in the National Museum collection, none of it is treated in detail. Some, but not all, of a large collection in the American Museum of Natural History from

this same field is also mentioned or discussed. In a few cases classification has demanded some detail concerning fossils from other collections and areas, especially the San Juan Basin, in New Mexico, notably in dealing with the genera *Claenodon* and *Anisonchus*.

Most of the new genera and species recognized in the course of this work were named, with brief diagnoses, in a preliminary note abstracted from the first draft of part 2 (Simpson, 1935d). These diagnoses are here repeated, in some cases in emended form, and accompanied by the extended discussion and description omitted in the preliminary paper. There is included a full discussion of the fossil Primates, even though these have already been published in some detail (Gidley, 1923).

In the course of preparation of this bulletin, I have had access to and have made constant use of a memoir on the Paleocene of the San Juan Basin by the late Dr. W. D. Matthew. This has now been published by the American Philosophical Society, but it was available only in manuscript throughout the course of my work. Reference to it is made by the citation "(Pale. Mem.)." Other citations are by author and year and refer to the "Literature cited" at the end. As far as possible without destroying the comprehensive and unified character of this work, I have avoided any duplication of material contained in Matthew's memoir. For groups that he also discusses I have generally omitted diagnoses and have confined discussion to a brief summary and to those points wherein I differ from him.

Throughout this work, wherever they proved useful, statistical methods have been employed. These are all summed up in Fisher (1925) and also in a paper soon to be published (Simpson and Roe). The methodology is outlined here in connection with the first group treated, the Multituberculata. In all the statistical figures given, the stated error is standard, not probable. The following abbreviations are consistently used throughout for brevity, along with the universally understood symbols for teeth.

L=Length.

W=Width.

N=Number of specimens in a given sample.

R=Range.

M=Mean.

$\sigma$ =Standard deviation.

$d/\sigma$ =Deviation from a specified mean, divided by the corresponding standard deviation.

$V$ =Coefficient of variability= $\frac{100\sigma}{M}$ .

P=Probability.

$t$ =A constant for comparing small samples } {as defined  
by Fisher.

$\Sigma(d^2)$ =Sum of the squares of deviations from the mean.

In the systematic zoological part of this work, it has not seemed necessary in each case to give the evidence or arguments for associations of upper and lower dentitions. With very few exceptions these collocations are not based on actual association of upper and lower jaw remains of one individual, which is very rare in this field. It is based rather on occlusion, occurrence at the same localities, relative abundance, comparison with related forms from other fields, and similar indirect but usually conclusive criteria. In the few cases where there is any serious doubt about the association, this fact is mentioned.

This manuscript was completed on March 15, 1936. Slight changes have since been introduced, but no later general revision has been made, and with few exceptions statements made are to be taken as of that date.

#### HISTORY OF THIS STUDY AND ACKNOWLEDGMENTS

Work for this memoir was started in 1908, when Dr. T. W. Stanton commissioned Albert C. Silberling to collect Fort Union fossils for the United States Geological Survey and the United States National Museum. In 1909 Dr. J. W. Gidley visited the field, where he directed and planned further work by Silberling, and he also then undertook the laboratory and office work on the collection. In view of the extremely fragmentary and few fossil mammals that had been collected in the Fort Union up to 1908 and the general scarcity of mammals of comparable age from any formation, the magnitude to which this work would grow could not have been anticipated when it was started. In 1911, when Mr. Silberling finished his most intensive work on this collection (to which he also added periodically until 1932), he had brought together one of the largest collections of Paleocene mammals ever made. Furthermore, this collection consisted almost entirely of new species, more than half the genera were new, and it greatly extended morphological and distributional knowledge of the families and orders represented. The collection represented, potentially, the greatest single contribution to knowledge of early mammals that had ever been made.

The very magnitude of the results achieved was embarrassing. All these hundreds of specimens had to be prepared, the majority of them by tediously working off the matrix grain by grain under a microscope. Concurrently with many other duties, this was undertaken by Dr. Gidley, and it occupied much of his time over a period of 12 years. Then the identification of the material presented great difficulties, as it must in any Paleocene collection, for on one hand all the genera and species are clearly variable and on the other the really significant characters are often in such small details that it may be difficult to distinguish forms properly classified in different orders.



These difficulties were enhanced by the fact that the most pertinent comparative material was in another institution and that Dr. Gidley's other duties did not permit his spending the months, or even years, of comparative study necessary under these circumstances, except by short visits or the loan of a few specimens as opportunity presented.

In spite of the really tremendous amount of work that he had accomplished on the collection, Dr. Gidley was able to complete only a relatively small part of the final preparation and publication of manuscript before his death on September 26, 1931. Up to the end, he looked forward to the completion of the work, and remarked, in conversation, that the collection was the most important ever in his hands and that its publication would be his greatest contribution to science and his most enduring monument. This it is, despite the fact that he was not spared to complete it with his own hands.

In 1932, Dr. Alexander Wetmore and C. W. Gilmore invited me to undertake the completion of this study. The officers of the American Museum of Natural History permitted the use of my time, as a cooperative undertaking with the United States National Museum. The whole collection was shipped to New York, where it could be studied under the best possible circumstances and compared at first hand with almost all the other types of American Paleocene mammals. Knowledge of the field, and further accessions to the collections, were made possible by work with Mr. Silberling in Montana for the National Museum in 1932 and for the American Museum in 1935.

The great extent of Dr. Gidley's contribution to this work should be explicitly stated.<sup>1</sup> In the first place, the existence of this splendid collection is in large part due to him. He collected some of the best material, and he directed and encouraged the collection of most of it. Second, he prepared and cataloged the whole collection so that it came to me in almost perfect condition for immediate study. Third, he prepared and published four preliminary papers (as listed in the bibliography and discussed in the proper places in the text). It is inevitable that some differences in point of view and more particularly the lapse of time make complete agreement impossible, but his preliminary work greatly facilitated study of the groups involved. Fourth, a number of unpublished illustrations had been prepared under Dr. Gidley's direction, and most of them appear in this publication. Finally, he left a few notes on the unpublished parts of the collection.

There is reason to believe that Dr. Gidley had the major outlines of the classification of the collection, and probably also many of its details, well in mind. This preliminary orientation is one of the longest and most difficult parts of research, but unfortunately Dr. Gidley did not find it necessary for his own use to reduce it to writing and

<sup>1</sup> For a review of Dr. Gidley's life and work see Lull (1932).



could not foresee how important this would have been for his successors. The available notes are thus fewer and less useful than was anticipated. Specifically, they are as follows:

1. A field notebook containing a list of 43 specimens collected by Gidley, with locality, horizon, and date, but no other data.

2. Illustrations and proofs of his paper on the Primates, with no unpublished data.

3. Notes on multituberculates and claeonodons, with no unpublished observations.

4. Twenty-seven pages of notes and of manuscript in various stages of preparation, with considerable duplication and different drafts of treatments of the same subject. These, the only unpublished original observations left by Dr. Gidley, include brief preliminary diagnoses of three new species of *Tetraclaenodon*, one of *Protogonodon*, one of *Mio-claenus*, one of *Tricentes*, one of *Mixodectes*, and one of a genus probably considered as new but not named or defined, and also a sketch diagnosis of a new genus and species of phenacodonts (here called *Gidleyina montanensis*).

As far as they can be deduced from these notes, I have mentioned Dr. Gidley's opinions in the present text. In some cases they warrant detailed discussion and quotation. In others, his notes were clearly of the most preliminary sort and would surely have been modified before publication, and in these cases it has seemed unjust to do more than mention them briefly. As regards the recognition of species, I first studied the collection independently and then ascertained whether any new species (or genera) recognized by me were anticipated in Dr. Gidley's notes. If they were, I credited them to Gidley, *ex ms.*<sup>2</sup>, and quoted sufficient of his diagnosis to establish his authorship. The species so recognized are *Deuterozonodon montanus*, *Mimotricentes latidens*, *Tetraclaenodon symbolicus*, and *Gidleyina montanensis*. Dr. Gidley's notes also include diagnosis of the genus *Gidleyina* but under a preoccupied name.

Some other new forms are recognized in the notes, but without a name or without a diagnosis or definite indication, so that Dr. Gidley could not technically be established as their author, but his recognition of them is mentioned. In a few cases I have been unable to agree that a form tentatively designated as new by Dr. Gidley is so, and then have pointed out this fact but have omitted his names in order not to create useless synonymy.

None of Dr. Gidley's notes were in such shape that it would have been just to him to publish them without revision, and in any event only a small part of this memoir is affected by his unpublished notes.

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<sup>2</sup> The International Rules of Zoological Nomenclature, Article 21, state that the author of a scientific name is he who first publishes it with a valid definition "unless it is clear from the contents of the publication that some other person is responsible for said name and its indication, definition, or description." This validates Gidley's authorship of these species published by me.

That this work has been written at all is largely due to Dr. Gidley, but he is not responsible for its errors or for any matter in it not explicitly stated to be his.

It is further desired to acknowledge how much this work owes to Albert C. Silberling, whose contributions to it go far beyond those usual from a collector. He discovered most of the fossil localities, including all those of real importance, and made far the greatest part of the collection, with skill, persistence, and devotion that cannot be too highly praised. He established a system of field records of the greatest accuracy, used throughout this publication. Even beyond this he so thoroughly examined the field and so carefully studied and correctly interpreted its geology that much of what is here written about it, and of what has appeared in publications by others, is merely reducing to writing observations made by or with him. He is thus in a sense an author and authority of the geologic part of this work, although he has not actually written any of it and is not responsible for misinterpretation of his views or observations. Aside from the long periods when he was definitely employed as a collector, Mr. Silberling has spent every spare moment for the past 35 years working in this field, and this memoir is in a real sense the outcome of this lifetime vocation and avocation.

The following illustrations were drawn by Rudolph Weber under Dr. Gidley's direction: Figures 22, 30-34, 37-41, 44*b* and *b'*, 59, 63*a*, 71*a* and *a'*, 72, 73*b*, 80.<sup>3</sup> The other drawings were made by Sydney Prentice, under my direction. The accompanying map is based on field work by Silberling and me and was drawn by John C. Germann. The field photographs were taken by me.

The late Prof. W. J. Sinclair, of Princeton University, lent and permitted the description of the specimens collected for that institution by Douglass and by parties under Farr. Dr. G. L. Jepsen has facilitated comparisons with specimens collected under his leadership for Princeton in the Fort Union of Wyoming. The Carnegie Museum, through J. J. Barke, lent material in their collection from this field. I am much indebted to these institutions and colleagues, as well as to officials of the United States National Museum, particularly Dr. Wetmore and Mr. Gilmore, for their support of the work and constant aid and encouragement, and of the American Museum of Natural History for the time and facilities provided.

#### PREVIOUS WORK

Discovery of Paleocene<sup>4</sup> mammals lagged behind that of typical faunas of any later epoch, or even of the Mesozoic. This slowness of discovery and the factors of scarcity of fossils and difficulties of study

<sup>3</sup> In a few cases Prentice has modified these drawings slightly.

<sup>4</sup> "Paleocene" is granted to be an epoch of the Tertiary, including post-Lance or post-Danian and pre-Gray Bull or pre-Sparnacian time.

to which it was due have made the subject of Paleocene mammals an obscure one, generally avoided, but they have also made it a particularly fruitful field for research in recent years.

The first Paleocene mammalian fauna to be discovered was that of the Thanetian, or particularly of its subdivision the Cernaysian, in France. *Arctocyon primaevus* was described by Blainville in 1841, but knowledge of the fauna really dates from Lemoine's publications beginning in 1878. It has only recently been revised and placed on a satisfactory basis by Teilhard (1916, 1921).

The American Puerco formation of New Mexico was named in 1875 but yielded no mammals until 1881, when the famous collector David Baldwin began a long collecting campaign there for Cope. This work has been followed, since 1892, by a series of expeditions to this field under Wortman, Granger, Sinclair, Simpson, and others for the American Museum of Natural History, which also acquired the Cope-Baldwin collection. This stratigraphic sequence in the San Juan Basin of New Mexico has become the standard of comparison for the Paleocene of the world, and its faunas are far the best known and represented by the most nearly perfect specimens (although in variety they do not exceed those to be described in this memoir). They have been described by Cope, Osborn, Earle, Wortman, Matthew, Granger, Simpson, and others and are thoroughly revised in a memoir by Matthew (Pale. Mem.), published while this bulletin was in press. Three quite distinct formations and faunas have been recognized, Puerco, Torrejon, and Tiffany, the first two each with two well-marked separate faunal zones of different facies but nearly the same age.

The Fort Union group was originally defined by Meek and Hayden (1861) as occupying "the country around Fort Union,<sup>5</sup> extending north into the British possessions to unknown distances; also southward to Fort Clark. . . . Seen under the White River group on North Platte River above Fort Laramie. Also on west side of the Wind River Mountains. . . . and also occupying extensive areas of country in Nebraska . . . and beneath the White River group at several distant localities." Although the designation of the type locality leaves no doubt as to the inclusion of certain strata in the group or as to its general position in the scale, the name has been used in many different ways, and in keeping with the spirit of the original description it has been applied to any or all strata at about this part of the geologic section, that is, in what we now call Paleocene, over a very large area in the Northwest. Thanks to this widespread occurrence or use of the name, and to the economic value of these rocks, especially as a coal-bearing series, few geologic formations have been more intensively and extensively studied. No general review of this work is here attempted

<sup>5</sup> Near the present site of Buford, N. Dak.



(see résumé and references in Thom and Dobbin, 1924) aside from the Crazy Mountain area and briefer mention of mammal discoveries elsewhere.

The earliest geological work in the particular area here under discussion appears to be that of W. H. Weed. In 1893 he mentioned the presence of about 4,000 feet of Fort Union sediments overlying his Livingston formation east of the Crazy Mountains. In the Livingston (Weed, 1894) and Little Belt Mountains (Weed, 1899) folios, he included the extreme western part of this area and referred to the presence of Fort Union here but mapped it all as Livingston. In an article on the Fort Union (Weed, 1896) he also discussed the Fort Union area in a general way and gave a section of part of these and of lower beds along Lebo Creek.

The first more detailed consideration of this area and the first adequate reference to its more important northeastern part was by Earl Douglass. In 1900 he worked here, principally in the Cretaceous but also in the Fort Union, where he collected leaves and invertebrates. In 1901 a Princeton University expedition was sent out under Dr. M. S. Farr, and Douglass accompanied this party and also continued work after they had left. The Princeton party traversed the Fort Union exposures, but most of their work of that season was in the Cretaceous. In August 1901, Douglass found the first mammals in this field, and the first ever discovered in the Fort Union, at two localities (5 and 6 of the lists given on a later page) near the northern end of Bear Butte. Although fragmentary and few, these sufficed to show the equivalence of these beds to the Torrejon of New Mexico (Douglass, 1902a). Douglass soon published detailed descriptions of the mammals and a discussion of the geology of the whole area (Douglass, 1902b). The Princeton party was also accompanied by Albert Silberling, then a boy of 16, who was destined to play the major role in the development of this field.

Princeton field parties, also under Dr. Farr and accompanied by Silberling, revisited the area in 1902 and 1903, and they then examined the Fort Union in more detail and found fossil mammals at a number of scattered localities and at widely different levels, from near the base of the formation to about 4,350 feet above the base and from the northeastern part of the field to the vicinity of Cayuse Butte, near the western margin of the principal mammal-bearing area. The fossils collected and observations made in 1902 and 1903 have never been published.

In 1905 Douglass made a long reconnaissance through Montana, and in the course of this he went northward from Bigtimber to Cayuse (or Melville) Butte. He noted the presence of the Fort Union over much of this traverse but did not add significantly to exact knowledge of the field. Apparently he had not been informed of the unpublished



discoveries of 1902 and 1903 on and around Cayuse Butte, and he found no mammals on his brief visit. His account of this trip (Douglass, 1909) includes a résumé of the geology of the area, involving also his observations in 1900 and 1901.

In the meantime Silberling had continued prospecting the field and had located the two richest known deposits, later developed as the Silberling and Gidley Quarries. He was for a time associated with the Carnegie Museum, to which Douglass had now also gone, and he sent in to it a small but important collection, principally from the Silberling Quarry. This was described by Douglass a few years later (Douglass, 1908) and was the basis of the first exact definition of mammals from this field, including the types of *Ptilodus montanus*, *Picrodus silberlingi*, *Coriphagus montanus*, and *Megopterna minuta*,<sup>6</sup> as well as many less exactly identifiable specimens.

In 1907 (see Stone, 1909) R. W. Stone worked in the northern part of this area for the United States Geological Survey, and in 1908 W. R. Calvert worked south of the area. They connected their observations west of the Crazy Mountains, and in 1909 also by reconnaissance east of the mountains and later published an important discussion of the Fort Union here and of its relations to the Livingston, applying the name Lebo to the lower part of the Fort Union (Stone and Calvert, 1910).

In 1908 Dr. T. W. Stanton visited the field, where he was accompanied by Silberling, who had in the meantime left the Carnegie Museum and started ranching in this area. They made detailed observations, including a section of the Lebo which I give on a later page, and Silberling was employed under Stanton's direction to collect for the United States Geological Survey and National Museum (Stanton, 1909). Knowlton had taken some interest in observations here, principally in connection with his placing of the Hell Creek and synchronous beds in the "Lower Fort Union" (see Knowlton, 1909), a view now universally abandoned and requiring no consideration here. In 1909, Stanton, Stone, Calvert, Knowlton, and M. R. Campbell briefly visited the area again to check certain critical localities, the results of their observations being principally given by Stone and Calvert (1910). Stanton (1914) and Knowlton (1914) later returned to their argument regarding the Cretaceous-Tertiary boundary, but with only incidental reference to this area.

Silberling continued the collecting begun in 1908 and spent much time in 1909, 1910, and 1911 collecting for the National Museum. It was in these years that he obtained most of the specimens described in this work. A few specimens collected in later years were also acquired by the National Museum, and Silberling has continually spent much time in the field, even when not commissioned by any

<sup>6</sup> Which is, however, invalid.

particular institution. In 1908 he had worked principally in the Silberling Quarry. In 1909 Gidley visited the field and then opened the Gidley Quarry at a site, Loc. 4, previously discovered by Silberling. Gidley himself collected many fine specimens here, and the work was continued by Silberling in 1909-11, and later, along with repeated prospecting of surface localities. In 1911 Gidley made another visit to the field.<sup>7</sup>

In 1909 Gidley described the splendid skull, jaws, and partial skeleton of *Ptilodus* that had been found in 1908 by Silberling in the Silberling Quarry. This is still the best multituberculate specimen in any museum, and the best single mammal specimen ever found in this field. Gidley continued the preparation of the collection, work done entirely by himself, as time and other duties permitted. This was completed in 1920. In the meantime two preliminary papers had been published, one on *Myrmecoboides* (Gidley, 1915) and one on the clacnodonts (Gidley, 1919). After the whole collection was prepared he began monographing it, but only the section on the Primates (Gidley, 1923) was completed or published. The extent of his unpublished work has already been noted.

In 1930 Silberling made a renewed examination of the field and also reopened the Gidley Quarry and made a collection that was purchased by the American Museum. In 1932, under the auspices of the National Museum (with the donation of my services by the American Museum), Silberling and I went over the whole area and adjacent regions, with the present work in mind. We then made the map (pl. 1) that accompanies this memoir and also made detailed stratigraphic observations. A small amount of material was collected, incidental to our visits to all the fossil localities, but no intensive collecting or quarrying was undertaken.

In 1935 the Third Scarritt Expedition of the American Museum, consisting of Mr. Silberling, a camp man, and me for the entire season, and Mr. and Mrs. Fenley Hunter, Dr. Walter Granger, and Albert Thomson for shorter periods, spent four months in this field, prospecting most of the surface localities, reopening the Gidley and Silberling Quarries, and developing a new quarry, named the Scarritt Quarry. The resulting collection, about equal in size to that here described, is in the American Museum. The material from the Scarritt Quarry has been described (Simpson, 1936b), and the results are here included in the general sections but not in the detailed descriptions. The surface material, which is relatively abundant and important but does not include any species not also present in the National Museum collection, has also been identified and is mentioned where apropos in the present work. The very large Gidley Quarry

<sup>7</sup> Gidley's statement (1923, p. 1) that he visited the field in 1908 and 1909 is probably a misprint, for it is contrary to Silberling's memory and to letters and other records that seem to show that his visits were in 1909 and 1911.

collection, and the few specimens from the Silberling Quarry, in the American Museum are not yet studied and do not enter into this study. For the most part they duplicate the collection described here.

Of other mammal discoveries in the Fort Union, the first of any importance was made by J. F. Lobdell in 1926 in a coal mine at Bear Creek, Mont. Collections were later made here for the Carnegie Museum and the American Museum and have been described by me (Simpson, 1928a, 1929a, b). The small but interesting fauna is of Upper Paleocene age, about equivalent to the Tiffany.

Discoveries in northern Wyoming, west of the Bighorn Mountains, have been of outstanding value. Sinclair and Granger (1911, 1912; also Granger, 1914) had found a fauna of Paleocene aspect here in beds which had previously been considered to be true Eocene and which they named Clark Fork. In 1927-29, Dr. G. L. Jepsen, working for Princeton University, found three distinct faunal horizons in (nominal) Fort Union strata beneath the Clark Fork in this area. He has shown that these correspond in age to the Puerco, Torrejon, and Tiffany, and hence has for the first time established a definite sequence of four distinguishable Paleocene mammalian faunas in a single continuous stratigraphic section (Jepsen, 1930). The faunas so far described are small but typical. Subsequent collecting under Jepsen at the same localities has yielded much more and better material, but the results have not yet been published.

Sporadic discoveries of one or two specimens have been made at a few other Fort Union localities, but none is of much importance. The type of *Titanoides primaevus* came from near the type locality of the group, Buford, N. Dak. (Gidley, 1917). Typically Middle Paleocene forms, *Tetraclaenodon* and *Pantolambda*, were found in Billings County, N. Dak. (Lloyd and Hares, 1915). In Fort Union or Kingsbury beds of the Bighorns a jaw identified by Gidley as *Tricentes* was found (Stanton, 1909, p. 268). Eocene fossils were found in supposed Fort Union beds in the Powder River Basin (Wege-mann, 1917). The last-mentioned fossils, and perhaps that from the Kingsbury, are not really from the Paleocene, or from true Fort Union.

The Paskapoo of Alberta, which may be considered in a general way a northern extension or equivalent of at least the upper part of the Fort Union, has yielded a few mammals, the first found by Brown in 1910 (Simpson, 1927), with later discoveries mostly by Russell (1926, 1929, 1932), all extremely fragmentary. Recently Patterson, working for the Field Museum of Natural History, collected fine skeletons of *Barylambda*, an ally of *Titanoides*, at an Upper Paleocene level in the Plateau Valley formation of western Colorado (Patterson, 1933, 1934, 1935, 1937).



## PART 1: GEOLOGY AND FAUNAS

### GEOGRAPHY

The region here primarily considered is comprised in Tps. 3-6 N. and Rs. 13-16 E. (Montana principal meridian), an area of about 575 square miles. It is approximately included in latitude  $45^{\circ}55'$  to  $46^{\circ}20'$  N., longitude  $109^{\circ}40'$  to  $110^{\circ}10'$  W., and is in central Montana, Tps. 3-5 N. in Sweetgrass County and T. 6 N. in Wheatland County. The principal commercial center is Harlowton, seat of Wheatland County, 8 miles due north of the designated area. This town, population about 1,500, is on the north side of the Musselshell River and is a division point on the main line of the Chicago, Milwaukee, St. Paul, and Pacific Railroad. About an equal distance south of the area is Bigtimber, population 1,200, on the south bank of the Yellowstone River. The only settlement in the limited region here primarily treated is Melville, an old town once of some importance but now reduced to little more than a post office and crossroads store. It is in secs. 11 and 14, T. 4 N., R. 14 E.

There are main east-west motor highways and railroads in the Musselshell and Yellowstone Valleys, north and south of this area, but just here east and west through travel is blocked by the impassable mountains immediately to the west. There is, however, a secondary north-south highway from Harlowton to Bigtimber through the area, and this is now being improved and graveled (1935). There are several county roads, graded but unsurfaced, as shown on the map, and also many private roads and wagon trails, which permit approach to within a mile or less of any point in the field.

Much of the land has been plowed for dry-land wheat raising, but a great deal of it was not suitable for this purpose and so most of the wheat farms have been abandoned. A little wheat and some hay or alfalfa are still raised, but most of the region is given over to grazing, mainly as winter range for sheep and some cattle. The population is sparse and in recent years has not been prosperous. There are a few dude ranches in and near the mountains in the western part of the field. There are no known mineral resources.

Topographically the area lies immediately east of the Crazy Mountains, a very rugged and beautiful isolated range 25 or 30 miles long, north to south, and 10 to 15 miles in width, rising to 11,178 feet in Crazy Peak. The area specifically treated extends from the foothills of the mountains eastward about 25 miles. The divide between the Musselshell and Yellowstone Rivers runs through the field. The northern part is drained mostly by Fish Creek, here running eastward,











and its southern part mostly by Sweetgrass and Otter Creeks and their tributaries, here running mainly southeastward. The extreme northwestern part is drained by American Fork and Lebo Creeks, tributaries of the Musselshell, and the extreme southwestern part by Bigtimber Creek, tributary to the Yellowstone. Lebo and Fish Creeks rise in this area and carry little water in ordinary weather, while the other streams mentioned rise in the mountains and have larger and more nearly permanent flow.

Apart from the actual mountain area and its flanking zone of pediments, moraines, and outwash, here poorly developed, this region is a hilly one with mature topography almost entirely determined by the hardness and structure of the underlying rocks. The harder sandstones form ridges and scarps, and the softer beds are eroded into valleys or flats. The most striking elevations in the northeastern part of the field, like Bear Butte and Lion Butte, are sandstone-capped erosion forms. Cayuse Butte, a prominent but relatively low and irregular mass, and Porcupine Butte, the most prominent elevation outside the mountains, also are supported by intrusive igneous rocks (as are the mountains). The southern part of the field is hilly but has no prominent topographic features. There are three small lakes in the area, Lebo Lake in the northwest and Lakes Adam and Walvoord (more generally known as the Glass Lindsay Lakes) in the southeast, all artificial and developed for irrigation.

The highest point outside the mountains is Porcupine Butte, 6,970 feet, and the lowest is on Fish Creek where it leaves this area, about 4,000 feet.

Climate and vegetation vary from mountain to high-plains types. The mountain flanks have forest of lodgepole pine and other conifers, with aspens along the streams and some colorful meadows, while the main part of the field is very sparsely timbered, with evergreens on the higher sandstone ridges and cottonwoods in wet valley bottoms. The broad intervening areas, except for the relatively small irrigated patches, are characterized by sagebrush, pricklypears, small yuccas, and grass. Abandoned plowed land is taken over by weeds, especially Russian thistles. In spite of the rather sparse nature of the vegetation, almost the entire area is sodded over. Shale exposures are small and relatively few, and there are no badlands.

The topography along the northern edge of the area (beyond the Fort Union exposures) is very different, for here there are large, well-developed, high, gravel-covered terraces cutting across the tilted Cretaceous beds without regard for their hardness.

This general Fort Union area has received various designations, such as "Fish Creek", "Bear Butte", "Sweetgrass County", or "Melville." Fish Creek is a minor stream draining less than half of the region especially considered. Bear Butte is a small and marginal

topographic feature. Sweetgrass County does not include some of the most important localities, and does include a vast area, much of it south of the Yellowstone, far outside that here treated. Melville is an unimportant settlement local to one small part of the field. This whole region, a great synclinal area with Fort Union rocks filling it, may be called the Crazy Mountain region, for these mountains occupy its approximate center and are the most prominent topographic feature in this part of the State, and the major structure has already been called the Crazy Mountain Syncline. The smaller area designated and discussed above is, in general, the eastern half of the Crazy Mountain region, and is that where the Crazy Mountain Fort Union is best and most clearly developed and where it has yielded mammals. This area will herein be called the Crazy Mountain Field.

## GEOLOGY

### STRATIGRAPHY

#### GENERAL STRATIGRAPHIC COLUMN

Rocks exposed in the area between the Musselshell and Yellowstone Rivers and east of the Crazy Mountains are from Lower Cretaceous to Recent in age. Aside from terrace gravels, moraine and outwash deposits, valley fill, and other unconsolidated young deposits, not to be considered here, the sedimentary rocks are Cretaceous and Paleocene, as far as definitely established. There are numerous igneous intrusions, all younger than the Paleocene sediments, and likewise omitted from this discussion. The whole stratigraphic column, including some rocks not exposed in the area of the map (pl. 1) but all within a few miles of these and undoubtedly underlying this area, may be summed up in a general way as shown in the column on page 15.

From exposures outside this area, especially in the Big Snowy and Belt uplifts, it appears that the sedimentary rocks here exposed are probably underlain by many thousands of feet of earlier Mesozoic, Paleozoic, and pre-Cambrian sediments, probably one of the thickest piles of sediments in the world.

The oldest surface beds of this region are exposed only in the centers of domes north of the mapped area, for instance in sec. 34, T. 7 N., R. 16 E. Dr. Barnum Brown has recently obtained some interesting dinosaurs from this locality. There is some question whether these beds are closer to the Kootenai or to the approximately equivalent Cloverley, but here they have generally been called Kootenai.

The series here called "Undifferentiated Colorado" is probably susceptible to definite subdivision and correlation, but this has not yet been clearly accomplished and is outside the scope of the present study. The lower part was given the local name "American Fork" by Douglass (1909), who called the upper, marine, beds "Fort Benton",



|                        |                    |          |                                                                                                                                                                         |                               |
|------------------------|--------------------|----------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------|
| Fort Union             | No. 3              | Melville | Dark shales, greenish or gray, with numerous gray to yellow sandstones. Mammals, etc.                                                                                   | 5,000+ feet.                  |
|                        | No. 2              | Lebo     | Soft somber greenish sandy shales and gray sandstones. Mammals, etc.                                                                                                    | 850 feet.                     |
|                        | No. 1              |          | Somber shales with some hard brown sandstones. Mammals, etc.                                                                                                            | 500 feet.                     |
| ?Fort Union (or Lance) | Bear               |          | Alternating pale cross-bedded sandstones and shales. Rare turtle bones, etc. No dinosaurs or mammals.                                                                   | 500-600 feet.                 |
| Hell Creek             |                    |          | Pale, variegated clays with some gray sandstone. Dinosaurs.                                                                                                             | 2,000 feet.                   |
| Lennep                 |                    |          | Brown and yellow sandstone and some somber shale. Transitional marine-fresh-water.                                                                                      | 250-450 feet.                 |
| Bearpaw                |                    |          | Soft dark shales. Marine. (Also some dinosaurs.)                                                                                                                        | 700-1,100 feet.               |
| Judith River           |                    |          | Cross-bedded gray sandstone and sandy shale. Dinosaurs.                                                                                                                 | 400-800 feet.                 |
| Claggett               |                    |          | Brownish or yellowish thin-bedded sandstones and shales. Marine to brackish invertebrates.                                                                              | 400-800 feet.                 |
| Eagle                  |                    |          | Three prominent coarse white sandstones. Coal.                                                                                                                          | 100-250 feet.                 |
| Colorado               | (Undifferentiated) |          | Upper part soft dark shales, locally sandy. Lower part with much thin-bedded and ripple-marked sandstone. Upper part marine, lower with dinosaurs, turtles, and plants. | 1,300-2,000 feet.             |
| Kootenai               |                    |          | Variegated red, green, and brown shales and sandstones. Dinosaurs and nonmarine mollusks.                                                                               | 300+ feet (base not exposed). |

probably an inexact correlation. Probably equivalents of the Mowry, Thermopolis, Frontier, and some other Wyoming formations are included. A prominent but local sandstone member has been called "Big Elk."

Douglass at first (1902) called the overlying beds "Niobrara", but their more exact correspondence with the Eagle and Claggett is

now well established. In 1902 he applied the name "Fish Creek Beds" to the next higher division but later accepted their equivalence to the Judith River as established by Stanton and Hatcher (1905). Douglass (1909) continued to use the name "Fish Creek" for beds transitional between Judith River and Bearpaw, but this name is not now in general use.

Lennepe is a local name applied by Stone and Calvert to beds perhaps equivalent to the Fox Hills but not definitely correlated. In physical character they resemble the Lebo, and seem to grade into the Livingston laterally.

#### CRETACEOUS—TERTIARY TRANSITION

It is not proposed to discuss here the general evidence for drawing the boundary between the Cretaceous and the Tertiary, a problem to which this field contributes only one small part, and not the most important part. For present purposes it is assumed that beds up to and including the true dinosaur-bearing Lance and Hell Creek and their equivalents belong in the Cretaceous and that overlying beds without dinosaurs (except by redeposition) and with mammals of Tertiary type (including carnivores, condylarths, etc.), from the Puerco and its equivalents upward, are to be placed in the Tertiary. It is also assumed that the Paleocene is accepted as a separate epoch of the Tertiary, of equal rank with the Eocene, Oligocene, Miocene, and Pliocene, and that its lower limit is taken as the base of the Puerco or equivalent, or the top of the (restricted) Lance or Hell Creek or their equivalents, and its upper limit at the top of the Clark Fork, or equivalent, or base of the Sand Coulee and Gray Bull, or equivalents.

On these assumptions, which I believe to be based on the most reasonable and useful interpretation of all the evidence, it is here proposed only to discuss briefly the beds in this field that must include the transition from Cretaceous to Tertiary as thus defined and to suggest where the boundary may occur in this local series.

The following is a somewhat generalized section from the Hell Creek into the Fort Union No. 1 in sec. 26, T. 6 N., R. 16 E., passing through Loc. 65 and near Loc. 78, about 2 miles northeast of the northern end of Bear Butte:

|                        |   |                                                                                                |                   |
|------------------------|---|------------------------------------------------------------------------------------------------|-------------------|
|                        |   | ----- Horizon of Loc. 78 -----                                                                 |                   |
|                        |   | Mostly greenish shales and sandy shales-----                                                   | <i>Feet</i><br>30 |
| Fort<br>Union<br>No. 1 | { | Somber cross-bedded sandstone, the upper part hard and ridge-<br>forming-----                  | 40                |
|                        |   | Somber greenish shale and sandy shale-----                                                     | 85                |
|                        |   | Same, with bone fragments including unidentifiable mammals<br>of Tertiary aspect, Loc. 65----- | 7                 |
|                        |   | Same, without fossils-----                                                                     | 35                |
|                        |   |                                                                                                | <hr/> 197         |

|      |   |                                                                                                              |           |
|------|---|--------------------------------------------------------------------------------------------------------------|-----------|
| Bear | { | Zone of hard brown concretions, with numerous fresh-water invertebrates and some turtle bones.....           | ± 1       |
|      |   | Transitional beds with shales somewhat darker than those below and with local lenses of brown sandstone..... | 15        |
|      |   | Alternating white cross-bedded sandstones and pale shales.....                                               | about 485 |
|      |   |                                                                                                              | about 500 |

|            |   |                                                                       |
|------------|---|-----------------------------------------------------------------------|
| Hell Creek | { | Softer beds, pale sandstone and clay, with dinosaurs-- (Not measured) |
|------------|---|-----------------------------------------------------------------------|

Definition of the new name "Bear" is given on page 20.

All these beds are tilted here, but there is no evidence of angular unconformity. The contact beneath the lowest hard sandstone of the Bear is sharp but not more so than beneath other sandstones throughout this series. Such a contact could, but does not necessarily, represent a parallel or erosional disconformity. The change from Hell Creek to Bear is, however, rather more abrupt than from Bear to Fort Union No. 1, the latter being transitional through a thickness of 15 to 20 feet, the boundary here taken by convention at a local shell lens.

Dinosaurs are found in place, apparently as originally deposited, at almost all levels in the Hell Creek, although no very good specimens have been found in this field. I have seen no dinosaurs in the Bear, but Mr. Silberling informs me that he has found isolated, rare, and very fragmentary specimens in the lower part of that formation, the highest being 80 feet above the base in this section. It is entirely possible that these few fragments were redeposited and derived from the Hell Creek. No dinosaurs have been found in the upper 420 feet of the Bear, but a few champsosaur and turtle bones and some invertebrates occur.

Invertebrates from the lens here considered as marking the top of the Bear have been identified by Dr. L. S. Russell as follows:

|                                                  |  |                                                  |
|--------------------------------------------------|--|--------------------------------------------------|
| ? <i>Fusconaia danae</i> (Meek and Hayden).      |  | <i>Viviparus formosus</i> Meek.                  |
| ? <i>Nedionidus senectus</i> (White).            |  | <i>Campeloma nebrascense whitei</i> Russell.     |
| <i>Elliptio priscus</i> (Meek and Hayden).       |  | <i>Campeloma limnaeiforme</i> (Meek and Hayden). |
| <i>Viviparus trochiformis</i> (Meek and Hayden). |  | <i>Physa cf. canadensis</i> Whiteaves.           |

Dr. Russell remarks that the three pelecypods range widely in the Northwest, Judith River to Fort Union, and that the species of *Viviparus* characterize the Fort Union and equivalents (listing mainly Upper Paleocene levels), the two *Campelomas* are likewise from the Fort Union or equivalents, and the *Physa* is of little significance. He concludes that the "fauna contains nothing characteristic of the Lance and includes several species restricted to the Fort Union. It can be regarded with some confidence as Paleocene in age."



As already noted, there are no exactly identifiable mammals from Loc. 65, but the fragments found here are of Tertiary rather than Cretaceous aspect, and the mammals from Loc. 78 are certainly Paleocene and probably Middle Paleocene. It seems probable that the whole Fort Union No. 1 here is of Middle Paleocene age and all but certain that it does not include the earliest Paleocene.

There are two possible interpretations of this section. First, the usual view, in analogous cases, that the Bear is Cretaceous, equivalent to part of the Lance, with the necessary corollary here that part of the Paleocene, a Puerco equivalent, is probably lacking. This interpretation is possible, but it seems to me decidedly the less likely of the two. The invertebrates indicate Paleocene and probably not earliest Paleocene. Even if it be decided that they should be considered basal Fort Union rather than uppermost Bear, they are intimately associated with the latter and in beds that grade into it insensibly. This gradation itself opposes this interpretation, for it makes the presence of an unconformity here, or a gap representing Puerco time, seem unlikely. If a break exists it is more likely to be within or below the Bear. The absence of dinosaurs, with the presence of such reptiles as did survive into the Tertiary, in most of the considerable thickness of the Bear is also evidence against this view, negative but of some weight.

The second possible interpretation is that most of or all the Bear belongs in the Paleocene, probably representing the Lower Paleocene, and that the Cretaceous-Tertiary boundary is in its basal part or below it. All the items of evidence mentioned above favor this view. Opposing it are the possible presence of dinosaur bones in the basal Bear and the absence of mammals. The dinosaur fragments are, however, such as could very readily be redeposited from erosion of the Hell Creek, and they are confined to the lower 80 feet of a series about 500 feet thick. It is entirely possible that there is a disconformity, or at least a valid epoch boundary, in this series at the base of a sandstone above the level of these bones, and still more likely that the dinosaur bones are not really original fossils in these beds. The absence of mammals has no weight. Mammals are rare throughout the field as a whole, are generally excessively rare in the Lower Paleocene, in this field almost never occur in sandstone, which is all that is well exposed here, and even if present would be small forms easily overlooked. The absence of dinosaurs, however, may well be significant, because their bones are large, occur in most terrestrial Cretaceous formations, and are very likely to occur where, as here, there are remains of other types of reptiles.

Another summary section through the whole Hell Creek and Bear was taken in sec. 15, T. 6 N., R. 15 E. This is continuous with the lower Fort Union section of Stanton and Silberling given elsewhere.



| ----- Base of Fort Union No. 1 -----                 |                                                                                                                     | Feet   |
|------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------|--------|
| Bear                                                 | Clays with thin and inconstant sandstones, a more prominent sandstone at the top not well exposed here-----         | 280    |
|                                                      | Gray to buff platy sandstones in beds usually one to three feet thick, with thicker shale partings-----             | 330    |
|                                                      |                                                                                                                     | 610    |
| Hell Creek                                           | Pale variegated shale with occasional soft blocky sandstones_                                                       | 765    |
|                                                      | Pale gray sandstone-----                                                                                            | 10     |
|                                                      | Mainly pale variegated sandstone-----                                                                               | 270    |
|                                                      | Heavy gray sandstone, with some shale-----                                                                          | 145    |
|                                                      | Pale white to greenish clays with brown concretionary layers, sandstones increasingly prominent toward the top----- | 660    |
|                                                      |                                                                                                                     | 1, 850 |
| ----- Base of Hell Creek -----                       |                                                                                                                     |        |
| Yellow Sandstone and Sombre Clay----- (Not measured) |                                                                                                                     |        |

Dinosaurs are found in the Hell Creek in this region also, but no animal fossils were found in the Bear.

The discrepancy in thickness of the Bear between this section and that previously given, about 110 feet, seems too great to be due entirely to difficulty of accurate measurement and is probably at least in part a real difference. The localities are about 8 miles apart in a straight line. It is also possible that the limits taken do not exactly correspond in the two sections, as all the formations concerned are highly variable.

Knowlton (in Stone and Calvert, 1910, p. 749) reports the following leaves from "200 feet below the top of the Lance Formation", that is, in the Bear at this locality: *Sapindus affinis*, *Sapindus grandifoliolus*, *Platanus aceroides*, *Platanus* sp.?; and the following from a level still lower by 200 feet, probably still in the Bear: *Sapindus ?grandifoliolus*, *Sapindus* sp., *Platanus raynoldsii*. Knowlton unreservedly called these Fort Union, but this has no bearing on the question here considered, since he also called true Hell Creek and Lance floras Fort Union. All these species are reported from beds probably of Lance age, but they are all equally characteristic, or considerably more abundant, in the true Fort Union.

Throughout the northern part of the field at least, and generally except where all the subdivisions of this part of the section tend to merge indistinguishably into the Livingston, the beds between the Hell Creek and the Fort Union No. 1, or basal Lebo, are a good lithologic unit. The scanty data also suggest a distinctive paleontological character. These facts and the possibility, or as I believe probability, that the beds should be classified as Paleocene, or associated with the Fort Union, rather than as Cretaceous and associated with the Hell Creek or "Lance" make it highly advisable to distinguish

them by a separate name, and I have here called them "Bear",<sup>8</sup> from Bear Butte around which they are typically developed. They may perhaps be equivalent, approximately, to the Tullock, but this would be an assumption that might result in serious misapprehension. They are far removed from and discontinuous with the type Tullock, into which it will never be possible to trace them, and their lithologic character is not the same. It is improbable that they are exactly equivalent to the Tullock, and even if this should prove to be the case it would seem warranted and necessary to retain for them a local name. At present correlation with the Tullock would be only a guess, which might well prove to be incorrect.

Typical exposures of the Bear are shown in plate 2.

#### FORT UNION

The use of the name "Fort Union" has been so loose and ill-defined that it has become necessary for every writer who uses it to propose his own individual definition or to run the risk of being completely misunderstood. In general it has been applied to beds in the Dakotas, Montana, and Wyoming, in the northwestern high-plains region (and in part intermontane areas) that are, or are supposed to be, later than the Lance and earlier than the Wasatch. This apparently satisfactory definition is in fact most indefinite. In the first place, there has not always been general agreement even to this extent, Knowlton, for instance, placing beds generally referred to or correlated with the Lance in the "Lower Fort Union." In the second place, the definition is dependent on that of Lance and of Wasatch, which are themselves very ill-defined. It is certain in some areas (notably Polecat Bench in northern Wyoming, as shown by Jepsen) and probable in most or all that strata generally referred to the Lance, often under the name of Tullock but not necessarily equivalent to the type Tullock, are in reality distinctly later than the typical Lance or the equivalent Hell Creek and both faunally and stratigraphically are more nearly related to the overlying beds, that is, to the Fort Union. Thus even aside from the question of accurate recognition of the boundaries and correlation of members of these formations and groups, there is often doubt as to which group should include a given member. The time-honored name "Wasatch" is still more ambiguous, to the point that very few of the beds called "Wasatch" are really equivalent to any part of the type Wasatch. Granted that the use of the name is usually intended to imply approximate correlation with the Gray Bull, there still remain many doubts as to its proper contents, for there is generally a thick series of beds, Tiffany, Clark Fork, and so on, that are some-

<sup>8</sup>I am indebted to Miss M. Grace Wilmarth, of the U. S. Geological Survey, for informing me that "Bear" and also "Melville" (defined on a later page) are not included in her records as ever having been used previously as the names of stratigraphic units.

times included in "Wasatch", sometimes in Fort Union, and sometimes are separated from both as an intervening stage.

As a matter of personal opinion, I would prefer to use "Fort Union group" for the whole Paleocene series of this northwestern plains area, to include all strata of age equivalent to or intermediate between the Puerco and the Clark Fork. This usage is very broad, but the designation "Fort Union" has already been so loosely applied that a more restricted usage would be very difficult to frame or to maintain. It at least has the virtue of being on the whole a natural subdivision of the Tertiary and of including practically all the beds that have ever been called Fort Union, except in out-and-out error or in such wholly untenable classifications as that of Knowlton. For more precise work it will in any case be necessary to define and use more local names for particular formations and members included in the Fort Union group.

In this field, the earliest workers recognized as Fort Union only the beds from the basal No. 3 sandstone (as defined on a later page) upward. Douglass, Stone and Calvert, Stanton, and all later workers, however, have also included the underlying andesitic beds called Lebo by Stone and Calvert. The name "Fort Union" is used throughout the present study for the Lebo and all higher early Tertiary strata in the area here considered. The uppermost part of this series is of unknown age and may possibly be as young as the Gray Bull, in which case it should be removed from the Fort Union, but at present no evidence warrants this step. In addition there is a series of strata, the Bear, hitherto always considered as Cretaceous and referred to the Lance, but in my opinion possibly Tertiary. If it should prove to be Tertiary, I would place it in the Fort Union, but this is now doubtful, and in this study the word "Fort Union" is not intended to include the Bear.

The local Fort Union, thus defined, includes three mappable lithologic units of very unequal thickness. Mr. Silberling, who first recognized these units, has applied numbers to them, with Fort Union No. 1 at the base and No. 3 at the top, and his field designations have been employed in publications by Stanton, Osborn, Gidley, and others. In accordance with the general rules of stratigraphic nomenclature, local geographic names are here applied, but throughout this discussion I shall also employ Silberling's numerical designations. The correspondence is as follows:

$$\text{Fort Union} \begin{cases} \text{No. 3} = \text{Melville (new name).} \\ \text{No. 2} \\ \text{No. 1} \end{cases} = \text{Lebo.}$$

The No. 1 and No. 2 beds are generally similar, and both are included in the Lebo of Stone and Calvert, but they are easily sepa-



rable throughout the field, and their distinction makes discussion and records more exact. Both are said to be in large part andesitic, and both are characterized by their somber color, the shales generally greenish and the sandstones dark brown, gray, or gray-green.

The No. 1 beds, or lower Lebo (shown in pl. 2), are characterized by numerous lenses and beds of hard and resistant dark sandstone, so that this unit is generally topographically positive and forms a ridge or series of ridges. This characteristic is visible throughout the field; for instance, typically in the gentle anticline in the northern part of T. 5 N., Rs. 15-16 E., where the No. 1 forms an elevated hilly area surrounded by a horseshoe valley developed on the No. 2 beds. The upper limit of the No. 1 is taken at the top of the highest and most persistent of its hard sandstones. The thickness, as measured in secs. 15-22, T. 6 N., R. 15 E., is 496 feet (Stanton and Silberling). It has not elsewhere been accurately measured. It may be somewhat thicker in the western and thinner in the eastern parts of the field but apparently does not vary greatly.

The No. 2 beds are topographically negative (see pl. 3). They form valleys between the No. 1 and No. 3 sandstones, or slopes beneath the latter. The characteristic material is greenish shale, often rather coarse and sandy, with lenses and beds of gray sandstone. When unweathered, these sandstones may be hard, for instance in the overburden of the Gidley Quarry, but they weather rapidly and are not resistant to erosion. It is this nonresistant nature of its sandstones, and generally their somewhat lighter color, that distinguish this member most sharply from the No. 1. The thickness in the measured section mentioned above is 840 feet and probably averages 800 to 900 feet throughout the field. Stone and Calvert (1910, p. 753) give a total thickness of 2,080 feet for the Lebo on Lebo Creek. I did not measure the beds here (where they are not very well exposed and have a variable and uncertain dip) but estimated the thickness at not much over 1,500 feet, with about 600 feet in the No. 1 and 900 in the No. 2. They give a total thickness of the Lebo in T. 6 N., R. 16 E. (that is, near the north end of Bear Butte) of only 463 feet, which I think is surely much too small. It is highly unlikely that this persistent formation thins out from 1,334 to 463 feet in less than 8 miles. The dip in this region changes rapidly, as the beds are around the Bear Butte syncline, and exposures are not continuous, so that exact measurement is not possible, but it is unlikely that the thickness is much if any less than 1,200 feet here, with some 700 or 800 in the No. 2 and 500 or 400 in the No. 1.

The Lebo as a whole forms a narrow band along the northern edge of the field, from the northeastern end of the Crazy Mountains almost due east, but with some sinuosity, to sec. 23, T. 6 N., R. 15 E. Here they turn abruptly southward, and their exposure widens greatly



under the influence of the Widdecombe Creek anticline, the axis of which is mostly on the lower Lebo, with the upper Lebo forming a horseshoe valley around it, the eastern limb being occupied by Widdecombe Creek. The exposures then swing around the northern end of Bear Butte (with the No. 2 also continuous through the gaps across the axis of the Bear Butte syncline) and then swing southward and widen until they form a very wide area of low relief in the vicinity of the Glass Lindsay lakes (Lake Adam and Lake Walvoord). The upper limit against the No. 3 swings abruptly westward in sec. 34, T. 4 N., R. 15 E., and runs over to the Crazy Mountains, which it reaches some 17 or 18 miles south of its northern departure from those mountains. The exposure as a whole thus forms a great loop closed on the west by the mountains, as shown in plate 1.

The No. 1 and No. 2 beds seem to be perfectly conformable and to intergrade, forming a natural unit, sandier in its lower part, so that the single name Lebo for both is acceptable. In the northern part of the field they are generally sharply separable, but in the south it is often difficult to distinguish them. It is to be noted, however, that in this southern area they are nearly horizontal and are very poorly exposed and that in this direction all subdivisions, even between undoubted Cretaceous and Tertiary, tend to break down or to be very difficult to distinguish.

The best exposed section showing the whole thickness of the Lebo is in secs. 15-22,<sup>9</sup> R. 6 N., T. 15 E., where it has been measured by Stanton and Silberling who give the following section (Stanton, 1909, p. 263, here slightly modified):

|       |                                                                                                                                                                                                           |                |
|-------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------|
| No. 3 | { Massive sandstone-----                                                                                                                                                                                  | (Not measured) |
|       |                                                                                                                                                                                                           | <i>Feet</i>    |
|       | { Shale with a few thin bands of sandstone-----                                                                                                                                                           | 112            |
|       | { Gray sandstone-----                                                                                                                                                                                     | 5              |
|       | { Shale-----                                                                                                                                                                                              | 18             |
| No. 2 | { Gray limestone, weathering brown [a concretionary layer, not a continuous stratum]-----                                                                                                                 | 3              |
|       | { Greenish-gray somber shale with much soft sandstone of same color and brown . . . concretions in lower third, a few thin bands of sandstone in upper part and several concretionary zones near top----- | 700            |
|       |                                                                                                                                                                                                           | 838            |
|       | { Brown, thinly cross-bedded sandstone forming . . . ridge-----                                                                                                                                           | 32             |
| No. 1 | { [Somber greenish] shale-----                                                                                                                                                                            | 200            |
|       | { Greenish-gray sandstone-----                                                                                                                                                                            | 15             |
|       | { Greenish-gray shale-----                                                                                                                                                                                | 249            |
|       |                                                                                                                                                                                                           | 496            |

A section of the underlying beds at this same locality is given on a previous page.

<sup>9</sup> Stanton says sec. 15, but the greater part of the beds are here in the adjacent sec. 22.

Stone and Calvert and others have given other sections, but they are too generalized or include too many unexposed parts to be very helpful.

The Fort Union No. 3 beds (see pl. 6) are a great mass at least 4,000 feet thick, and possibly as much as 6,000 if the highest strata of this series in the Crazy Mountains be included. Determinable fossils are known only from the lower 3,000 feet, and this is the part to which attention has been particularly directed. In spite of the great thickness and heterogeneity, there is no convenient lithologic or paleontological basis for subdividing the beds. They consist of shales and sandstones, most of them lenticular and highly variable. The usual topographic expression is a series of ridges on the sandstones and valleys on the shales. The shales, particularly at the mammal localities, do not differ greatly from those of the No. 1 and No. 2 in appearance, but the sandstones are lighter in color and are generally more resistant than those of the No. 2. Since the shales are poorly exposed, the general impression is of a much paler formation than the underlying Lebo. The massive basal No. 3 sandstone is the most continuous and prominent horizon marker in the Fort Union of this field and has been remarked by everyone who has worked here. It almost everywhere forms a prominent scarp, and its resistance to erosion is the cause of the elevation of Bear Butte, Lion Butte, and numerous less notable hills and escarpments.

The base of this sandstone forms a natural division plane throughout the field and is evidently an erosional disconformity, although it is unlikely that it marks any considerable time gap. The sandstone tends to become less massive in the southern part of the field toward the south end of Lion Butte and where it swings westward to the mountains, and it is here generally more platy and formed by numerous thin beds with shale partings but can be traced continuously almost to the mountains.

The fluviatile nature of these beds and the presence of numerous channel and flood sandstones make it possible that there are disconformities at almost any level, but none can be detected as of any regional significance, and the whole series seems to be essentially continuous and without any noteworthy or sudden change in general type of sedimentation.

The base of the No. 3 is further made noticeable, especially from the air, by almost everywhere supporting a growth of evergreens (pls. 3, 5). This is the more noteworthy because the sandstones of the No. 1 beds, even where almost identical with those of the No. 3 in topography and elevation, do not support any trees, and the Lebo in general is almost devoid of large vegetation except for cottonwoods along the stream courses.

The No. 3 beds occupy an irregular area, somewhat more elongate east and west than north and south, bounded by the Crazy Mountains on the west and by the loop of Lebo exposures on north, east, and south (pl. 1).

From their position over the Lebo, it may be supposed that the No. 3 beds correspond in their lower part to the Tongue River and perhaps in their upper part to the Sentinel Butte, but such a correlation is at present totally unwarranted. They are very distant from the typical or from any unquestionable exposures of the Tongue River or Sentinel Butte, their lithology is no more like either Tongue River or Sentinel Butte than like many other formations and certainly is not close enough, in itself, to warrant correlation without tracing them laterally continuously or nearly so into true Tongue River and Sentinel Butte, which is impossible. Their age is well established, in part, as brought out below under "Correlation", but that of typical Tongue River and Sentinel Butte is not, and paleontological correlation with those members is not now possible.

Under these conditions it is certainly less helpful than conducive to serious error to adopt the frequent practice of assuming that a correlation exists. Still worse is the practice, also exemplified by some work on the Fort Union, of assuming that both Tongue River and Sentinel Butte must occur here and dividing the beds, in which no natural division has been established in the field, according to the proportionate thickness of these members in a widely different area.

I therefore propose the local name Melville for the lithologic unit, from the town of Melville, which is situated on these beds and is surrounded, within a few miles, by excellent and typical exposures of them. The lower boundary of the formation is well established, as shown on the accompanying map. The upper boundary is still uncertain. The name is proposed to include at least the lower 3,000 feet of the No. 3 beds, to about the top of Cayuse Butte, and tentatively for the whole No. 3 of this field, to the highest sediments on Porcupine Butte. Later discoveries might make it advisable to remove some of these uppermost strata from the formation, and the pertinence of still higher beds around the mountain flanks is wholly dubious.

Concretions are common throughout the Fort Union here. Limy concretions, weathering rusty yellow, may be of great size, up to 10 feet or more in greatest diameter, and locally characterize a definite stratum, but these appear to be truly concretionary and not a true sediment or limestone. Shell limestones do occur locally in the No. 3 beds, but in the No. 1 and No. 2, while shells may be fairly abundant in relatively small lenses, they are generally in a shale matrix and do not form a true limestone. In the No. 3 beds there are a few thin bands of comminuted shells, or shell breccia (notably at the Scarritt Quarry), generally mixed with clay.



The relatively small quantity of carbonaceous material is noteworthy in all three subdivisions. There are a few thin impure and local lenses of coal in the No. 3, and a little prospecting has been done on these, but none are of any commercial value. Aside from these thin seams, generally only an inch or two thick, there are a few carbonized tree trunks, occasional very local lenses of coal a few feet in diameter and less than an inch in thickness, and locally many minute carbon fragments and filaments. In marked contrast with the Fort Union of most other areas, these rocks can be classed as not coal-bearing.

Several workers, especially Stone and Calvert and Silberling and I, have attempted to follow out the development of this Fort Union series into regions beyond the local field, but with indifferent success. To the eastward it ends against the Cretaceous, and the Fort Union reappears, considerably modified in thickness and character, after a long gap, in the Bull Mountain Field (see Woolsey, Richards, and Lupton, 1917; also Ellis and Meinzer, 1924). The lower part of the Fort Union is there predominantly a shale member, dark and greenish in color, with some sandstone (not closely similar to that of the No. 1 in the Crazy Mountain Field) and coal, about 200 to 300 feet in thickness. This is commonly correlated with the Lebo, which is probable on lithologic grounds, but there is no evidence that it represents the whole Lebo or that it is not a lithologic facies of somewhat different span in time. The correlation is here more probable than in any other area where the Lebo is supposed to occur, but it cannot be considered as established beyond doubt. The upper part of the Fort Union is here only 1,650 feet thick and contains more pale shale, more and different limestone, more numerous and persistent hard sandstones above the base, and much more coal than does the No. 3 of the Crazy Mountain Field. The Bull Mountain Fort Union is an isolated mass, completely surrounded by Cretaceous outcrops.

The Fort Union encircles the Crazy Mountains, which are formed principally by intrusive masses thrust into it, and has been followed in some detail by Stone and Calvert (1910). (Silberling and I have also made a reconnaissance around the mountains on which, as well as on Stone and Calvert, my remarks are based.) The Upper Cretaceous formations and the Lebo, steeply folded and much disturbed and altered by later igneous activity, swing around and into the northeastern end of the mountains. The Hell Creek here appears to contain more andesitic debris and comes to resemble more closely the Lennep and the Lebo. Toward the southwest, and southward on the western flank of the Crazies, the Hell Creek, Bear, and Lebo have not been distinguished. It seems probable that they here merge lithologically with the Livingston, as Stone and Calvert believe, or they may possibly be absent. There remains, however, the possibility

that more detailed study and discovery of fossils, especially vertebrates, would permit their differentiation here. West of the mountains the late Cretaceous and early Tertiary strata are thrown into a series of folds, roughly parallel to the mountain flank and with north-south trend. There is no wide zone of Fort Union, as east of the mountains, but strata lithologically similar to the Fort Union do occur in narrow zones, as folded. Some of them are almost identical in character with the Melville beds of the eastern flank and include abundant leaves. This Fort Union facies, overlying the Livingston, also occurs in the southern part of the mountain area, but it is much disturbed and poorly exposed and not enough work has been done to trace its continuity with the well-differentiated series in the north-eastern area. It is probable, as Stone and Calvert suppose, that it includes only the upper part of the Fort Union of the latter region. No mammals have been found in it.<sup>10</sup> There is a large area lithologically like the Melville around the southeastern flank of the mountains also, but here again exact correlation is impossible at present, and considerable search has not yet revealed any mammals or other fossils indicative of exact age.

The Fort Union exposures are surrounded by older rocks throughout the northern and western areas, and no extension or correlation of the beds in these directions is possible.

Following the beds southward, the division between the No. 1 and No. 2 tends to break down, and this is probably true also of that between the Hell Creek, Bear, and No. 1 Fort Union near the Yellowstone River. The beds here take on a violet hue, especially the shales, a color also seen in the northern area but there rare and here predominant. The indivisible beds so colored apparently include the Lebo, probably the lower part of the Melville, and also extend down into the Cretaceous—that is, this part of the series is blending into the undivided Livingston, as reported by Stone and Calvert.

There is a dark sandstone that may represent part of the No. 1 Fort Union skirting this area and visible near the 4,700-foot contour on the south of the divide between the Yellowstone and Stillwater Rivers, south of Reed Point, and also apparently at Absarokee, but the identification is uncertain. If this is the No. 1, it represents the farthest point to which a definite subdivision of the Crazy Mountain Fort Union can really be traced, even in this highly dubious fashion, as far as I have been able to ascertain. We were unable to establish any continuity with the Red Lodge or Polecat Bench areas, and lithologically the beds in those areas are not comparable to those of the Crazy Mountain Field, nor are similar subdivisions recognizable.

<sup>10</sup> About 1910 a sheep herder showed Mr. Silberling a jaw of an animal similar to *Pantolambda* that he said was found near the head of Shields River, or between it and Potter Creek. It was impossible to obtain the specimen for exact identification or to verify its reported origin.

They include nothing really comparable with the Lebo, and the resemblance to the Melville is too vague to have any real correlative value. Paleontological correlation alone seems to have any significance between this region and that near the Crazy Mountains.

#### STRUCTURE

The beds of this field are almost nowhere exactly horizontal and in places are steeply tilted. Even in the course of purely paleontological work it is necessary to take strict account of the structure, since relative levels between the numerous isolated exposures can seldom be measured directly but have to be calculated from the structural data.

Along the north side of Fish Creek, from the mountains eastward to sec. 23, T. 6 N., R. 15 E., there is a strong monoclinal flexure dipping south at angles of about  $40^{\circ}$  to  $75^{\circ}$ . North of this fold only Cretaceous beds are exposed. The flexure itself involves the uppermost Cretaceous, Bear, Lebo, and basal Melville. The strike is sinuous but is mainly east and west to the end of the Crazy Mountains, where the Melville beds mostly run into that range, while the lower beds swing around its northern end. In the section noted, this fold ceases to affect the Fort Union beds, which are affected south and southeast of here by a broad anticline with northeast-southwest trend and low dips up to about  $12^{\circ}$ . Erosion along the axis of this anticline has formed a great embayment, about 6 miles wide at its mouth and of about the same depth, north and south, surrounded by a high rim on the basal Melville. Widdecombe Creek flows along the soft No. 2 zone on the eastern limb of the anticline. Directly east or southeast of this anticline is a parallel syncline the axis of which is occupied by remnants of the basal Melville sandstone rising abruptly above the No. 2 slopes and valleys. Puet Creek cuts deeply into this, separating the axial elevation into the long isolated Bear Butte to the northeast and Lion Butte, to the south and connected with the great mass of No. 3 beds extending westward to the mountains.

The Hell Creek, Bear, and Lebo swing around the north end of Bear Butte, dipping toward it. The dip increases in intensity here away from the actual Butte, until in the upper Hell Creek northeast of the Butte it reaches about  $30^{\circ}$ . The Lebo flanks the long east scarp of Lion Butte with low dips, usually  $4^{\circ}$  or  $5^{\circ}$ , toward the latter, variable and affected by slight local disturbances. South of here, toward the Glass Lindsay Lakes, the Lebo is nearly horizontal, with dips up to  $1^{\circ}$  or  $2^{\circ}$ , erratic in direction but oftener to the west.

Over the greater part of the Melville beds area, south of the strong monocline and west of the Widdecombe Creek anticline, the dips are prevailing westward and fairly consistent at  $4^{\circ}$  or  $5^{\circ}$  over a large



area, to the western part of T. 5 N., R. 14 E. Here the wide pass between Porcupine Butte and Cayuse Butte is in the very broad, poorly marked syncline or basin. The beds around Porcupine Butte dip northeasterly into this area, although in the Butte itself the dip (about 5°) is nearly north.

There are a few visible small faults with a throw of a few feet, such as one at the Silberling Quarry, but these are negligible in beds of such great thickness. No faults of sufficient importance to show on the map or to affect stratigraphic leveling significantly were detected.

The deformation appears to have been entirely post-Fort Union, and nowhere in this region was any angular discordance detected between the various Cretaceous and Tertiary formations, even down into the Lower Cretaceous (Kootenai) in the domes north of this area. It is a reasonable assumption that the deformation was approximately contemporaneous with the post-Paleocene igneous intrusions.

## FOSSIL LOCALITIES AND FAUNAL LISTS

### GENERAL OCCURRENCE OF FOSSIL MAMMALS

Fossil mammals, represented at least by material adequate to show its mammalian nature, have so far been found at 57 localities in this field, of which about 35 have yielded material sufficiently well preserved for generic identification, and about 25 material specifically identifiable and of some real value in correlation and faunal studies. The great bulk of the collections comes, however, from the three localities where quarries have been developed.

Although some of the more resistant sandstones, such as those in the No. 1 beds or the basal sandstone of the No. 3 beds, are well exposed and form more or less continuous outcrops wherever they occur in the field, the finer and less resistant sandstones and the shales and clays are on the whole very poorly exposed. Bones are occasionally found in the sandstones, but they are there very rare and are generally of no value. Only one identifiable mammal has ever been found in a true sandstone in this field. The mammal localities are therefore almost entirely on the rarer shale exposures, which occur where coulees have cut the shale slopes or where the wind has developed blow-outs. Such exposures, seldom as much as a hundred yards in diameter and generally much less, are limited in number. In the productive area in this field there are probably not over 400 of them, and all of these have been prospected by Mr. Silberling, many of them also by me or others.

The mammal occurrences may be grouped under two categories, as surface localities or as (actual or potential) quarries. At the surface localities, much the more numerous of the two, the mammal remains are rare, as far as known, and are so sparsely scattered through the matrix that only accidental finds or concentration from long weathering and wind erosion leads to any production. The ideal conditions

at such localities are deep weathering *in situ* without erosion or surface drift or wash, combined with gentle deflation, which removes the small weathered shale particles but leaves the larger or heavier fossils. Such conditions are relatively rare, and it is also noteworthy that numerous localities that were in good collecting condition when first found 30 years or so ago have now lost much of their value or promise by drifting over of windblown material or surface wash, by the spread of vegetation onto their weathered surfaces, or by active erosion, which removes the surface concentrates and leaves only a clean, hard shale exposure in which there is little chance of finding a fossil *in situ*.

The quarry localities are those where fossils are so concentrated in a local pocket that it is profitable to work the bed as a whole and recover fossils in place. The difference is, of course, of degree and not of kind but is one of great practical importance. Were it not for its three principal quarries, which have been called the Gidley, Silberling, and Scarritt Quarries, this field would be of relatively little importance. There are marginal localities also of some importance, intermediate between quarries and straight surface localities. Thus Loc. 81 (as listed below) was literally a quarry, but the whole bone pocket and therefore quarry was only about a yard in diameter. Loc. 25 has yielded so much surface material that a concentration of probable quarry calibre is indicated, but the rather limited attempts made to quarry at that locality have not in fact developed a profitable bone layer.

An outstanding characteristic of the field, regardless of level or geographic position, is the fragmentary nature of the material. In the hundreds of specimens collected, there are so far known only four or five mammal specimens complete enough to be called skulls, and only two of these really adequately reveal most of the skull structure. Only about 10 specimens include associated upper and lower teeth, and only three any surely associated limb bones. Nothing approaching a complete skeleton has ever been found. This fragmentary condition is seen not only in the surface specimens but equally in those found *in situ* deep in the quarries. The quarry specimens commonly show fresh breaks that look recent and yet abut against undisturbed matrix. It is also peculiar that most of the quarry specimens had lost some of their teeth before burial and that jaws quite devoid of teeth are relatively abundant.

For his own records and in connection with the National Museum collecting, Mr. Silberling has numbered every locality where any fossils were found. These serial numbers are here adopted and are those used throughout the present work. There are now 82 numbered localities; 25 of these are not mammal localities, but for completeness and the convenience of later workers they are all given in the serial list on a later page. The map (pl. 1), however, shows only mammal localities.

## THE GIDLEY AND SILBERLING QUARRIES

The greater part of the National Museum collection, about four-fifths of the identifiable specimens, is from the Gidley and Silberling Quarries, of which the Gidley Quarry is far the more important, with nearly seven times as many specimens as the Silberling Quarry.

The Silberling Quarry, Loc. 1, was located, as a surface prospect, by Mr. Silberling in 1902, and he subsequently made a small collection here that formed the basis of Douglass' publication in 1908. In 1908 Silberling opened the quarry for the National Museum and then collected most of the specimens known from this locality. In 1909 the much richer and more easily worked Gidley Quarry drew his attention away from the Silberling Quarry, and little work has since been done there. Silberling has done some further prospecting, however, and in 1935 the Third Scarritt Expedition reopened the quarry and worked it for a few days, but abandoned it on finding the bed bone poor, the stripping very difficult, the fauna essentially duplicating that of the Gidley Quarry, and the matrix unsatisfactory from the point of view of preparation. This quarry did, however, produce the splendid *Ptilodus* skull and partial skeleton described by Gidley, and it is the only locality in this field where *Psittacotherium* or *Elpidophorus minor* have been found. All its other genera and species are represented by about equally good or better material from other localities.

The Silberling Quarry is in NE $\frac{1}{4}$ SW $\frac{1}{4}$  sec. 4, T. 5 N., R. 16 E., in an embayment near the middle of the east side of Bear Butte (see pl. 5). The fossil horizon is about 75 feet below the base of the No. 3 sandstone and is the highest level in the No. 2 that has yielded identifiable mammals. The bone layer is not well defined by any visible criteria but is limited to a zone 1 or 1 $\frac{1}{4}$  feet in thickness. The matrix is a fine greenish tuff or shale, very tough and harsh, extremely abrasive to handle, and difficult to work in preparation. It grades laterally into a bed with numerous fresh-water bivalves, among which mammals also occur, but this matrix is so hard that preparation of fragile specimens would be almost impossible.

The Gidley Quarry, Loc. 4, is in NW $\frac{1}{4}$ NE $\frac{1}{4}$  sec. 25, T. 5 N., R. 15 E. (see pl. 4). It is immediately adjacent to the county road, on its east side, where it descends the steep hill from the basal No. 3 rimrock to the valley of the upper part of Widdecombe Creek, on the relatively unresistant and topographically negative No. 2 beds. A small coulee here descends the slope, in a westerly direction, and cuts the bone bed apparently near the middle of the rich pocket in which the Gidley Quarry is developed. The locality was discovered by Mr. Silberling as a surface prospect in this coulee in 1905. When Dr. Gidley visited the field in 1909, Mr. Silberling showed him this locality as the most promising of any in the field. The surface



material was unusually abundant but so disintegrated as to have little value. Dr. Gidley dug in along the bone stratum until firmer material was found in place, made a good collection from this bed, and thus started the quarrying operations that Silberling and others have continued intermittently ever since. Mr. Silberling's operations for the National Museum, resulting in the bulk of the collection here described, consisted in stripping and working out an area of about 1,400 square feet (a very rough estimate). The other important operation, that of the Third Scarritt Expedition in 1935, extended over an area of about 1,750 square feet (also a rough approximation, as the area was irregular and not all uncovered at once).

The quarry consists of two cuts, one north and one, of smaller size, south of the coulee and original surface exposure. The material collected by Silberling was carefully labeled as to the cut from which it came, but in this study there was found to be no significant difference between the two parts of the collection, and it is all treated as a unit. The greater part of the worked-out area has been filled in again in later stripping, and the cuts left open weather and fill rapidly, so that the form of the quarry is not apparent in the field. The north section has probably been about worked out, except for a probably very rich corner left under heavy overburden. The south section was still rich along the margin as left in 1935 and probably would produce over an area of at least 1,000 square feet, and possibly 1,500, before the bone layer ran out into the hillside, so that the locality as left in 1935 is, as far as such things are predictable, still capable of producing another collection about as large as either of the two so far made there. The quarry has so far produced about 800 good identifiable mammal specimens and perhaps 1,500 single teeth and other unimportant fragments.

The areal distribution of the fossils is very erratic and patchy. In places it is possible to work for 1 or 2 days without finding any jaws, and in others one man can collect ten or more jaws in a day. In general, however, the fossils seem to be distributed in an elongated area, about 5 to 20 feet in width, usually nearer the smaller figure, and with a tested length of at least 150 feet, which probably will continue to a much greater distance. The general trend is north-northeast to south-southwest.

In many places the fossils are concentrated in a single and fairly well defined layer an inch thick or even less in which fragments of bone may be so numerous as nearly to make a bone-bed. This material is, however, very fragmentary, and good jaws are exceptional in it. In other places the bone layer is less definite, and the fossils are scattered more sparsely but generally in better preservation through a thickness of about a foot, or up to about 18 inches at most. Occasional fragments are found in the nearly barren material above and

below this more definite fossil horizon but (as far as observed) only within a few inches of it. The level is about 125 or 150 feet below the base of the No. 3 sandstone. Some additional remarks on the occurrence of fossils here are made in discussing the facies and ecology of the quarry fauna.

Table 1 gives a complete list of the fossils so far identified from the Gidley and Silberling Quarries, with the number of upper and of lower jaws of each species, based on the National Museum collection only except *Elpidophorus minor*, the one specimen of which is in the Princeton Collection. It is probably, but not quite surely, from the Silberling Quarry.

TABLE 1.—Fossil mammals so far identified from the Gidley and Silberling Quarries, Crazy Mountain Field, Mont.

| Species                                  | Gidley Quarry |            | Silberling Quarry |            |
|------------------------------------------|---------------|------------|-------------------|------------|
|                                          | Upper jaws    | Lower jaws | Upper jaws        | Lower jaws |
| <b>MULTITUBERCULATA:</b>                 |               |            |                   |            |
| Ptilodontidae:                           |               |            |                   |            |
| <i>Ptilodus montanus</i> .....           | 39            | 25         | 6                 | 11         |
| ? <i>Ptilodus douglassi</i> .....        | —             | 1          | —                 | 1          |
| ? <i>Ptilodus gidleyi</i> .....          | —             | 3          | —                 | —          |
| ? <i>Ptilodus sinclairi</i> .....        | —             | 14         | —                 | 4          |
| <i>Ptilodus</i> sp.....                  | —             | —          | 1                 | —          |
| ? <i>Ectypodus grangeri</i> .....        | —             | 5          | —                 | —          |
| ? <i>Ectypodus russelli</i> .....        | —             | 2          | —                 | 1          |
| ? <i>Ectypodus silberlingi</i> .....     | —             | 1          | —                 | —          |
| ? <i>Parectypodus jepseni</i> .....      | —             | 1          | —                 | —          |
| <i>Eucosmodon sparsus</i> .....          | —             | —          | —                 | 1          |
| <b>INSECTIVORA:</b>                      |               |            |                   |            |
| ?Deltatheridiidae:                       |               |            |                   |            |
| <i>Gelastops parvus</i> .....            | 1             | 3          | —                 | 1          |
| Leptictidae:                             |               |            |                   |            |
| <i>Prodiacodon concordiacensis</i> ..... | —             | 1          | —                 | —          |
| <i>Leptacodon ladae</i> .....            | —             | 13         | —                 | —          |
| <i>Leptacodon minusculum</i> .....       | —             | 1          | —                 | —          |
| <i>Myrmecoboides montanensis</i> .....   | 1             | 2          | —                 | —          |
| Nyctitheriidae:                          |               |            |                   |            |
| <i>Stilpnodon simplicidens</i> .....     | —             | 1          | —                 | —          |
| Pantolestidae:                           |               |            |                   |            |
| <i>Bessoecetor diluculi</i> .....        | 2             | 4          | —                 | 1          |
| <i>Aphronorus fraudator</i> .....        | 8             | 17         | —                 | 3          |
| Mixodectidae:                            |               |            |                   |            |
| <i>Eudaemonema cuspidata</i> .....       | 1             | 7          | —                 | 1          |
| <i>Elpidophorus minor</i> .....          | —             | —          | —                 | 1          |
| Picrodontidae:                           |               |            |                   |            |
| <i>Picrodus silberlingi</i> .....        | —             | 7          | —                 | 1          |
| <b>PRIMATES:</b>                         |               |            |                   |            |
| Plesiadapidae:                           |               |            |                   |            |
| <i>Pronothodectes matthewi</i> .....     | 1             | 8          | —                 | —          |
| Carpolestidae:                           |               |            |                   |            |
| <i>Elphidotarsius florencae</i> .....    | —             | 1          | —                 | —          |
| ?Anaptomorphidae:                        |               |            |                   |            |
| <i>Paromomys maturus</i> .....           | 6             | 32         | 1                 | —          |
| <i>Paromomys depressidens</i> .....      | 3             | 4          | —                 | —          |
| <i>Palaechthon alticuspis</i> .....      | 2             | 13         | —                 | 1          |
| <i>Palenochtha minor</i> .....           | 2             | 6          | —                 | —          |

TABLE 1.—*Fossil mammals so far identified from the Gidley and Silberling Quarries, Crazy Mountain Field, Mont.*—Continued

| Species                                    | Gidley Quarry |            | Silberling Quarry |            |
|--------------------------------------------|---------------|------------|-------------------|------------|
|                                            | Upper jaws    | Lower jaws | Upper jaws        | Lower jaws |
| <b>TAENIODONTA:</b>                        |               |            |                   |            |
| Stylinodontidae:                           |               |            |                   |            |
| <i>Conoryctes comma</i> .....              | 1             | -----      | 1                 | -----      |
| <i>Psittacotherium multifragum</i> .....   | -----         | -----      | 1                 | -----      |
| <b>CARNIVORA:</b>                          |               |            |                   |            |
| Arctocyonidae:                             |               |            |                   |            |
| <i>Claenodon montanensis</i> .....         | 1             | 2          | -----             | -----      |
| <i>Claenodon silberlingi</i> .....         | 1             | -----      | -----             | -----      |
| <i>Claenodon latidens</i> .....            | -----         | 1          | -----             | -----      |
| <i>Claenodon</i> sp.....                   | -----         | 1          | -----             | -----      |
| <i>Prothryptacodon furens</i> .....        | -----         | 2          | -----             | 1          |
| <i>Metachriacus punitor</i> .....          | 3             | 11         | -----             | 3          |
| <i>Spanoxyodon latrunculus</i> .....       | -----         | 1          | -----             | -----      |
| <i>Mimotricentes latidens</i> .....        | -----         | 4          | -----             | 2          |
| <i>Mimotricentes angustidens</i> .....     | -----         | -----      | -----             | 1          |
| Miacidae:                                  |               |            |                   |            |
| <i>Didymictis microlestes</i> .....        | 4             | 13         | 1                 | 1          |
| <i>Didymictis tenuis</i> .....             | -----         | 1          | -----             | -----      |
| <i>Didymictis phaydenianus</i> .....       | -----         | -----      | 1                 | -----      |
| <i>Ictidopappus mustelinus</i> .....       | 1             | 1          | -----             | -----      |
| Mesonychidae:                              |               |            |                   |            |
| <i>Dissacus</i> sp.....                    | -----         | 1          | -----             | 1          |
| <b>CONDYLARTHRA:</b>                       |               |            |                   |            |
| Hyopsodontidae:                            |               |            |                   |            |
| <i>Ellipsodon aquilonius</i> .....         | 17            | 34         | 1                 | 7          |
| <i>Litales disjunctus</i> .....            | 2             | 9          | -----             | -----      |
| <i>Litomylus dissentaneus</i> .....        | 2             | 3          | -----             | -----      |
| <i>Haplaletes disceptrix</i> .....         | 2             | 7          | -----             | -----      |
| Phenacodontidae:                           |               |            |                   |            |
| <i>Tetraclaenodon symbolicus</i> .....     | -----         | -----      | -----             | 1          |
| <i>Tetraclaenodon cf. puercensis</i> ..... | 2             | -----      | -----             | -----      |
| Periptychidae:                             |               |            |                   |            |
| <i>Coriphagus montanus</i> .....           | 1             | 6          | -----             | 1          |
| <i>Anisonchus sectorius</i> .....          | 4             | 3          | -----             | -----      |
| <b>PANTODONTA:</b>                         |               |            |                   |            |
| Pantolambdidae:                            |               |            |                   |            |
| <i>Pantolambda intermedius</i> .....       | -----         | 2          | -----             | -----      |
| <i>Pantolambda</i> sp.....                 | -----         | 1          | -----             | -----      |
| <b>TOTALS</b> .....                        |               |            |                   |            |
|                                            | 107           | 275        | 13                | 45         |
|                                            | 382           | 440        | 58                |            |

## THE SCARRITT QUARRY

The fauna of the Scarritt Quarry is not described in this memoir, being known only from material in the American Museum that has been published separately, but it is included in the faunal lists here given, and a general discussion is essential in the present consideration of the field as a whole. This locality, Loc. 56, was found by Mr. Silberling years ago and a few surface fragments collected. He located the bone layer and planned to attempt quarrying, but this plan was



not carried out until 1935, when the Third Scarritt Expedition opened a quarry here and made a collection of about 50 jaws and numerous teeth and odd fragments. The locality is in SE $\frac{1}{4}$ NW $\frac{1}{4}$  sec. 13, T. 5 N., R. 14 E., on the eastern slope of the low divide or spur that extends northward from Cayuse Butte. The horizon is estimated to be about 2,000 feet above the base of the No. 3 beds, hence about 2,150 feet above the Gidley Quarry and about 3,350 feet above the base of the recognized Fort Union of this area. As it is quite impossible to measure a continuous section between any of these datum planes, the horizon is approximate only but is probably of the right order, and the quarry is unquestionably much higher stratigraphically than the other quarries, and the highest in the field from which much identifiable material has been found except for Locs. 11 and 13, which are clearly higher, probably by about 1,000 feet.

The fossil level is marked by a bed, varying from a mere film up to about 4 inches in thickness, almost entirely composed of shell fragments. Mammals occur in this shell bed, and also in the clay (with more scattered and more complete shells) within 2 or 3 inches of it, both above and below. As far as the bone pocket has been followed, it is much less rich than the Gidley Quarry, but the material is good in average preservation and association of upper and lower jaws is relatively much more frequent than in the other quarries. (Four instances of association occur among the 50 jaws collected here, while such association has so far been found only once in the Silberling Quarry and once in the Gidley Quarry.) The fauna so far collected is as follows:

- Ectypodus hunteri*: 2 upper and 4 lower jaws and 27 isolated teeth.  
*Ptilodontid* undetermined: 1 tooth.  
*Leptacodon* cf. *tener*: 1 lower jaw.  
*Bessoecetor thomsoni*: 3 upper jaws, 9 lower jaws, and 1 specimen with associated upper and lower jaws.  
*Cf. Palaeosinopa* sp.: 1 tooth.  
*Elpidophorus patrus*: Associated upper and lower jaws, 1 upper jaw, 1 lower jaw, and 5 isolated teeth.  
*Unuchinia asaphes*: 1 lower jaw.  
*Plesiadapis anceps*: Associated upper and lower jaws and 6 isolated teeth.  
*Carpodaptes hazelae*: 1 upper and 3 lower jaws.  
*Phenacolemur frugivorus*: 1 lower jaw.  
*Cf. Chriacus* sp.: 1 tooth.  
*Litolestes notissimus*: Associated upper and lower jaws and 19 isolated lower jaws.  
*Tetraclaenodon* sp.: 1 upper molar.  
*Pantolambdoid* undetermined: 2 broken teeth and parts of limb bones.

#### OTHER IMPORTANT LOCALITIES

The following are faunal lists for and some notes on localities other than the three quarries that are of some importance. They include

all the localities for which mammalian material that can be identified is available, and also one locality of which this is not true but which is important as being the highest stratigraphically where mammal fragments have been found. All these localities merit repeated prospecting in the future, and any of them may turn up material of outstanding importance. The same is also true, but with less probability, of mammal localities, not especially discussed here but all given in the serial locality list, from which no identifiable specimens are now at hand.

FORT UNION No. 1, OR LOWER LEBO

*Loc. 65.*—Sec. 26, T. 6 N., R. 16 E. This is the lowest horizon at which mammals have been found in this field, being only about 35 feet above the base of the Fort Union No. 1, or of the Lebo. It is a small shale slope immediately north of the south line of the section and on the west side of a wagon trail that follows the base of the Fort Union No. 1, on the underlying sandstone ledge. The only identifiable mammal yet found here is a *P*<sub>4</sub> inseparable from *Ptilodus sinclairi*, mentioned in connection with the systematic description of that species. We have recently found here a few scraps of mammal bones, also crocodile or champsosaur teeth and ganoid scales, but the material is very scanty and poor. This is, nevertheless, the most promising prospect for obtaining material near the basal contact of the recognized Fort Union in this field.

*Loc. 78.*—Sec. 26, T. 6 N., R. 16 E. This locality is in the same section as Loc. 65 but farther west, on the other side of a sandstone-capped hill and at a higher level, about 200 feet above the base of the Fort Union No. 1. The only identifiable specimen yet found at it is the lower jaw made type of *Chriacus pugnax*.

*Loc. 9.*—Sec. 35, T. 6 N., R. 15 E. This is the most promising locality for mammals in the No. 1 beds. It is a good shale exposure on the west flank of the Widdecombe Creek anticline, about 200 feet below the base of the No. 2 and hence probably about 300 feet above the base of the No. 1, although this cannot be measured accurately. Search in 1935 revealed no new material. Previously the following had been collected: Lower jaw fragment of ?*Mimotricentes* sp., type upper jaw of *Claenodon recordensis*, and two upper molars (Princeton no. 13757) of *Tetraclaenodon ?symbolicus*.

*Loc. 73.*—Sec. 34, T. 6 N., R. 16 E. This locality is in the somber capping sandstone of the No. 1 beds, nearly 500 feet above their base. It has yielded only one mammal, a lower jaw of *Mimotricentes angustidens* in the Princeton collection. This is the only identifiable mammal to be found in a sandstone in this field. Subsequent search has not brought to light any other fragments at this locality.

## FORT UNION NO. 2, OR UPPER LEBO

The great bulk of the collection is from these beds. The Silberling and Gidley Quarries are described and their fauna listed in a separate section of this work. The other No. 2 localities with identifiable mammals are as follows:

*Loc. 51.*—Sec. 24, T. 4 N., R. 15 E. This is one of the richest of surface localities but has yielded no fossils in place. It is in the valley of Wildcat Creek, west of the stream, about 75 feet above the base of the No. 2 beds. The identifiable mammals are:

*Eucosmodon sparsus*: Lower incisor.

*Ptilodus ?montanus*: Broken premolar.

*Mimotricentes angustidens*: 2 isolated lower molars.

*Metachriacus provocator*: Associated upper and lower teeth, 2 isolated lower and 2 isolated upper jaw fragments.

*Metachriacus* sp.: Upper tooth.

*Didymictis* cf. *haydenianus*: Broken lower premolar.

*Ellipsodon aquilonius*: Lower jaw.

*Litaletes disjunctus*: Fragment of lower jaw and atypical but probably referable upper jaw.

*Tetraclaenodon* cf. *symbolicus*: Upper tooth.

*Anisonchus sectorius*: 4 lower jaws.

*Loc. 8.*—Sec. 23, T. 6 N., R. 15 E. The exact horizon is uncertain, but the locality is near Loc. 81 and probably at about the same or a somewhat lower level. The only identifiable fossil is a partial upper jaw of *Didymictis haydenianus*.

*Loc. 24.*—Sec. 2, T. 3 N., R. 15 E. This is near Loc. 25, about half a mile farther southwest, near the shore of Lake Adam, and at about the same level, about 300 feet above the base of the No. 2 beds. The identifiable mammals are: Associated upper and lower teeth of *Metachriacus provocator*, upper tooth of *Didymictis microlestes*, one upper and one lower jaw of *Anisonchus sectorius*.

*Loc. 25.*—Sec. 35, T. 4 N., R. 15 E. Near the north end of Lake Adam and about 300 feet above the base of the No. 2 beds. This is a rich locality that yields surface material on every visit, but only one specimen has been found in place and attempts to develop a quarry have so far been unsuccessful. The following have been found:

*Eucosmodon sparsus*: Lower incisor.

|                              |   |                              |
|------------------------------|---|------------------------------|
| <i>Deuteronodon montanus</i> | { | All known material.          |
| <i>?Deuteronodon</i> sp.     |   | See systematic descriptions. |
|                              |   | Five specimens.              |

*Metachriacus provocator*: 4 lower and 2 upper jaws (in American Museum).

*Tetraclaenodon symbolicus*: 9 lower and 1 upper (the upper and 4 lower in the American Museum).

*Anisonchus sectorius*: 3 lower and 1 upper (the upper in the American Museum).

*Loc. 50.*—Sec. 9, T. 3 N., R. 15 E. This is the southernmost locality in the field, southwest of Lake Adam. The horizon cannot be closely determined but is near that of Loc. 25. There is a large but



almost barren exposure at a small pointed hill and east of this a flat and poor but richer exposure where the following mammals were found:

?*Ptilodus gidleyi*: 1 lower premolar.

*Ptilodus montanus*: 2 lower premolars.

*Metachriacus provocator*: Associated upper and lower jaw fragments and 1 isolated lower.

*Anisonchus sectorius*: 1 lower jaw.

*Loc. 81.*—Sec. 23, T. 6 N., R. 15 E. This is in the extreme northern part of the field where the steep monocline swings into the Widdecombe Creek Anticline. It is in the lower half of the No. 2 beds, probably about 300 feet above their base. Mr. Silberling found this excellent shale exposure years ago, but nothing was found in it until 1935, when a small rich pocket of fossil mammals, most of them still in place, was discovered. Extensive prospecting failed to uncover anything else, and despite its richness this seems to have been a very local pocket, only 2 or 3 feet in diameter. The material is in the American Museum collection and includes the following forms:

*Aphronorus fraudator*: Upper premolar.

*Prothryptacodon ?furens*: 1 lower jaw.

*Metachriacus provocator*: 1 upper and 3 lower jaws.

*Mimotricentes ?latidens*: 1 upper and 1 lower jaw, possibly associated.

*Didymictis cf. haydenianus*: 1 upper jaw.

*Loc. 52.*—Sec. 23, T. 5 N., R. 15 E. This locality is at a large shale exposure immediately north of the Gidley Quarry. Fossils have been found here at two levels, one about the same as that of the Gidley Quarry and designated as Loc. 54, and the other, Loc. 52, about 50 feet lower. Numerous scraps have been found here, but the only certainly identifiable specimen is apparently associated right and left  $M_2$  and other fragments of *Claenodon montanensis*.

*Loc. 4.*—The Gidley Quarry occurs at this level relative to the other localities. It is discussed elsewhere.

*Loc. 5.*—Sec. 33, T. 6 N., R. 16 E. }

*Loc. 6.*—Sec. 34, T. 6 N., R. 16 E. }

These are the two discovery localities, where Douglass found the first Fort Union mammals in 1901. They are at nearly the same level, about 1,200 feet above the base of the Fort Union (No. 1), and 125 to 150 feet below the basal No. 3 sandstone, about the same level as the Gidley Quarry. Loc. 5 is a relatively large shale exposure on the west side of Bear Butte near its northern end, readily recognized as being opposite (across the county road from) a small, tepee-shaped outlier of the main butte. Loc. 6 is a smaller shale exposure about quarter of a mile northeast of Loc. 5 and just east, or slightly southeast, of the extreme northern end of Bear Butte (see plate 3). Douglass' material from the two localities (with identifications slightly amended in the light of later knowledge) was as follows:

*Tetraclaenodon* cf. *puercensis*: 3 isolated upper teeth.

*Ellipsodon aquilonius*: Jaw fragment with  $M_2$ .

*Anisonchus sectorius*: Jaw fragment with  $P_4$  and  $M_1$ .

*Pantolambda* spp.: Canine, premolar, and limb bones, perhaps of more than one species.

Subsequent discoveries at Loc. 5 include an unidentifiable multi-tuberculate and other fragments, and at Loc. 6 the following:

*Conoryctes* cf. *comma*: 2 upper molars.

*Tetraclaenodon* cf. *puercensis*: Upper jaw with  $dm^4-M^1$ .

*Pantolambda* sp.: Worn and broken upper molar and limb fragments.

Loc. 54.—Sec. 23, T. 5 N., R. 15 E. This is immediately north of the Gidley Quarry and at about the same level, on the same exposure as Loc. 52 but about 50 feet higher. The most nearly identifiable specimens found here are an isolated lower tooth and limb bones of *Pantolambda* sp. The rich pocket in which the Gidley Quarry is developed apparently does not extend this far north.

Loc. 1.—The Silberling Quarry is the highest mammal locality definitely in the No. 2 beds and occurs at this position relative to the other localities. It is discussed elsewhere.

Loc. 3.—On line between secs. 11 and 14, T. 5 N., R. 15 E. The horizon of this locality has not been determined, but it is in the upper part of the No. 2 beds. It has yielded only one lower jaw of *Tetraclaenodon symbolicus*.

#### FORT UNION No. 3, OR MELVILLE

This great upper division has numerous scattered localities, but only one (the Scarritt Quarry) has yielded a fauna that can be considered of much value. The first two localities here listed, 15 and 70, are definitely in the No. 3 beds, probably in their lower part, but of unknown relative level. The others are here arranged in the order of their stratigraphic levels.

Loc. 15.—Sec. 9, T. 5 N., R. 14 E. The only identifiable specimen from here is a lower jaw fragment indistinguishable from *Paromomys maturus*. The level is uncertain but is above the basal sandstone of the No. 3 beds.

Loc. 70.—Sec. 31, T. 6 N., R. 15 E. The only specimen from this locality, also in the No. 3 but of doubtful level, is a lower tooth probably of *Tetraclaenodon*, but possibly *Gidleyina*.

Loc. 82.—Sec. 11, T. 4 N., R. 15 E. There is some doubt about this locality, as the local section is not clear, but it is probably near the base of the No. 3 beds. The only identifiable specimen is associated  $M^2$  and broken  $M^3$  (in the American Museum) referable to *Tetraclaenodon* cf. *puercensis*.

Loc. 53.—Sec. 14, T. 4 N., R. 15 E. This locality is immediately adjacent to Loc. 82 and at the same level. It has yielded one upper tooth of *Claenodon* cf. *ferox*.

*Loc. 39.*—Sec. 15, T. 4 N., R. 15 E. This locality is also near the base of the No. 3 beds, and at about the same level as Locs. 82 and 53, possibly a little higher. Here were found a lower jaw fragment of *Claenodon cf. ferox* and limb bones probably of a pantolambdid.

*Loc. 12.*—Sec. 30, T. 6 N., R. 15 E. This locality is adjacent to the next, Loc. 27, and at a slightly lower level. It yielded an upper jaw of *Anisonchus sectorius*.

*Loc. 27.*—Sec. 30, T. 6 N., R. 15 E. This and Loc. 28 are at about the same level, 300 to 400 feet above the base of the No. 3 beds, on opposite sides of the Harlowton-Melville road where it turns after descending the "Fish Creek Hill."<sup>11</sup> The type material of *Gidleyina silberlingi* is from here.

*Loc. 28.*—Sec. 29, T. 6 N., R. 15 E. A little less than quarter of a mile northeast of Loc. 27 and at about the same level. It yielded an upper tooth of a pantolambdid and one identified as cf. *Conoryctes* sp.

#### PRINCETON LOCALITIES

Under this general heading I group numerous localities in the western part of T. 5 N., R. 15 E., and two in the northeastern part of T. 5 N., R. 14 E. The exact localities are given in the serial list and on the map. These localities were found and worked by the Princeton parties under Farr in 1902 and 1903 and were thoroughly prospected at that time, the surfaces apparently very well cleared. Mr. Silberling, Mr. Silberling and I, and the Third Searrith Expedition have at intervals between 1903 and 1935 gone over these localities again, but they have not yielded much new material. In the past few years their surface conditions have been increasingly unfavorable for collecting. Mr. Silberling's system of locality records was not initiated until several years after the Princeton work, and the locality records of the 1902 and 1903 collections, at least as they are now preserved, are very vague and not entirely reliable, especially as these parties also collected much material in those years at widely different levels in other parts of the field. There are a number of identifiable mammal specimens in the Princeton collections that can be definitely placed, on the basis of such records as are preserved and of Mr. Silberling's certain recollection of particular specimens, in a cluster of localities all at about the same level. Two more are possibly from this general area and level, but not definitely placed. The others (eight cataloged specimens) are surely or probably from quite different levels and localities and are mentioned elsewhere.

*Locs. 36, 38, 40, 41, 42, 43, 45, 57, 59, 60, and 68.*—All in secs. 17, 19, 20, and 29, T. 5 N., R. 15 E., all Princeton mammal localities, all at approximately the same level, stratigraphic differences probably not over 100 feet (which is generally insignificant in this field) and are

<sup>11</sup> As the road was until 1935, at least. Its course may be changed by work then in progress.



about 900 to 1,000 feet above the base of the Fort Union No. 3 or about 2,250 to 2,350 feet above the base of the Fort Union No. 1. The following Princeton material seems definitely to be from this group of localities.

*Gidleyina montanensis*: Type, as described below; this is from Loc. 68.

A lot including ?*Gidleyina* sp., lower premolar, a lower molar of an indeterminate oxyclaenine, and 3 probably associated lower teeth of *Anisonchus sectorius*, all probably from Loc. 42.

A badly broken lower jaw with 3 imperfect teeth, suggestive of *P. cavirictus* but not that species, perhaps not that genus, probably from Loc. 43.

*Gidleyina ?montanensis*: A miscellaneous lot including an M<sup>2</sup> probably of this species; an isolated P<sub>4</sub>. These are probably from Loc. 60.

The only approximately identifiable specimen now in the National Museum and labeled as from these localities, a lower jaw fragment from Loc. 57, probably *Gidleyina* sp. but possibly *Tetraclaenodon*.

Loc. 44 is at a slightly higher level than those just discussed, probably about 200 to 300 feet. It has yielded a large lot of probably associated material of *Claenodon ?ferox* and also an upper premolar probably pantolambdid but not *Pantolambda*. Both lots are in the Princeton collection.

Locs. 20, 61, 62, 63, 69 and 72 are also Princeton localities and have yielded mammals, but I have been unable definitely to tie in any identifiable specimens in the collections to these localities.

Loc. 56.—Sec. 13, T. 5 N., R. 14 E. This is the Scarritt Quarry, which occupies about this position relative to the other localities here listed. Its fauna is discussed elsewhere.

Loc. 18.—Sec. 14, T. 5 N., R. 14 E. This locality is nearly a mile west-southwest of the Scarritt Quarry, over a gentle hill (running north from Cayuse Butte), and at nearly the same level or perhaps a little higher. *Gidley* recorded it as "about 2,000 feet below the top of No. 3", and my estimates would place it at just about that distance stratigraphically below the highest exposures on Porcupine Butte. It has yielded a pantolambdid upper tooth, a lower jaw of *Anisonchus sectorius*, and a lower jaw fragment of *Ellipsodon* sp.

Loc. 11.—Sec. 23, T. 5 N., R. 14 E. }

Loc. 13.—Sec. 22, T. 5 N., R. 14 E. }

Although these localities are about half a mile apart at their ends and are in different sections, they are merely two parts of a series of shale exposures and blow-outs. Material from the two marked localities has not been consistently separated, nor is there any great need for doing so since they are at about the same level and in a more or less continuous series of exposures. They are high up on Cayuse Butte, or Cayuse Hills, on the divide between the Sweetgrass and Fish Creek drainages. Mr. Silberling has found numerous fragments on the surface here, and in past years the exposure has been good, but in 1932 and still more in 1935 we found it in poor condition, covered with wash and in places

tending to sod over. Efforts have been made to find a bone level or develop a quarry, but so far no material has been found in place. This series of exposures is important as the highest in this field from which identifiable material has been recovered. The level is about 3,000 feet above the base of the No. 3 beds. The National Museum specimens available are:

*Plesiadapis rex*: Type and referred material, as described below.

Cf. *Paromomys*, genus and species undetermined: An isolated upper tooth.

?*Gidleyina superior*: Type lower jaw.

*Tetraclaenodon* sp.: 2 upper molars.

To this list may be added the following forms in the Princeton collection. Their derivation from this level seems to be established with sufficient probability:

Multituberculate undetermined: 2 broken premolars.

*Elpidophorus* ?*patratus*: Lower molar.

*Claenodon* cf. *ferox*: 2 upper teeth.

*Thryptacodon* cf. *australis*: Lower molar.

Hyopsodontid aff. *Haplaletes*: M<sup>2-3</sup>.

Loc. 49.—NW $\frac{1}{4}$ NW $\frac{1}{4}$  sec. 23, T. 5 N., R. 14 E. This is near Locs. 11 and 13 in position and also stratigraphically. According to Mr. Silberling, Princeton no. 13756, numerous tooth and jaw fragments of *Claenodon* ?*ferox*, came from here.

Loc. 66.—Sec. 14, T. 5 N., R. 13 E. This is a very high exposure, at least 750 feet stratigraphically above Loc. 13, on the east flank of Porcupine Butte, about one-third of the way up that butte. It is a small shale exposure, important only as the highest level in this field where mammal fragments have been found. It is also considerably the most western mammal locality in the field. The material collected was, Mr. Silberling informs me, definitely mammalian, but probably was not identifiable and no specimens bearing this locality datum were found in the collection.

#### HORIZON UNCERTAIN

Here may be mentioned two Princeton specimens that are of too uncertain provenience for present inclusion in the more precise lists or for use in correlation.

No. 14191 includes two upper molars of a small *Claenodon*, comparable to *C. silberlingi*, collected July 3, 1903, labeled as from the Torrejon, "Anderson's Big Timber Road", a designation too vague to indicate any particular horizon or locality.

No. 13757, December 1902, "Loc. No. 9 Puerco", is probably from the Fort Union No. 1, since the No. 2 was known to be of Torrejon age by the Princeton parties and the No. 1 considered as Puerco. Loc. 9 of Silberling's series is in the No. 1, but since the Princeton parties did not use these numbers this is probably only a coincidence

and the locality is uncertain. The specimen includes  $M^{1-2}$  apparently of *Tetraclaenodon* and comparable to *T. symbolicus*, but not close enough to assure specific identification.

TABLE 2.—Serial list of localities, Crazy Mountain Field, Mont.

| No.     | Quarter                              | Section | Township North | Range East | Feet above base of Fort Union No. 1 | Remarks                                                       |
|---------|--------------------------------------|---------|----------------|------------|-------------------------------------|---------------------------------------------------------------|
| 1.....  | NE of SW.....                        | 4       | 5              | 16         | 1,265.....                          | SILBERLING QUARRY.                                            |
| 2.....  | NE half of NE quarter.....           | 7       | 4              | 16         | (In No. 2).....                     | "Various."                                                    |
| 3.....  | On line, near corner with 10 and 15. | 11-14   | 5              | 15         | (In No. 2).....                     | See faunal list.                                              |
| 4.....  | NW of NE.....                        | 23      | 5              | 15         | 1,200.....                          | GIDLEY QUARRY.                                                |
| 5.....  | SE of SE.....                        | 33      | 6              | 16         | 1,200.....                          | See faunal list.                                              |
| 6.....  | NE of SW.....                        | 34      | 6              | 16         | 1,200.....                          | Do.                                                           |
| 7.....  |                                      | 25      | 6              | 16         |                                     | (Not relocated—not a fossil locality).                        |
| 8.....  | Near middle of east half.....        | 23      | 6              | 15         | (In No. 2).....                     | See faunal list.                                              |
| 9.....  | SE of SE.....                        | 35      | 6              | 15         | 300.....                            | Do.                                                           |
| 10..... | ¼ mile south of north section lines. | 15-16   | 5              | 14         | (In No. 3).....                     | Mammal fragments.                                             |
| 11..... | SW of SW.....                        | 23      | 5              | 14         | 4,350.....                          | See faunal list.                                              |
| 12..... | SE.....                              | 30      | 6              | 15         | 1,700.....                          | Do.                                                           |
| 13..... | SW of SE.....                        | 22      | 5              | 14         | 4,350.....                          | Do.                                                           |
| 14..... | Same as Loc. 3.....                  | 11-14   | 5              | 15         | (In No. 2, a few feet below Loc. 3) | Mammal and other fragments.                                   |
| 15..... | NE of SW.....                        | 9       | 5              | 14         | (In No. 3).....                     | See faunal list.                                              |
| 16..... | NE of SW.....                        | 34      | 6              | 16         | 1,250.....                          | Invertebrates and mammal fragments.                           |
| 17..... | SE of NE.....                        | 15      | 5              | 15         | 1,400.....                          | Invertebrates.                                                |
| 18..... | NW of SE.....                        | 14      | 5              | 14         | 3,500.....                          | See faunal list.                                              |
| 19..... | NE of NE.....                        | 15      | 5              | 14         | (In No. 3).....                     | Mammal and other fragments.                                   |
| 20..... | NE of NE.....                        | 13      | 5              | 14         | (In No. 3).....                     | Invertebrates and <i>Claenodon</i> ( <i>vide</i> Silberling). |
| 21..... |                                      | 16      | 5              | 15         | (In No. 3).....                     | (Not relocated.) Invertebrates.                               |
| 22..... | SW of SW.....                        | 34      | 6              | 16         | (In No. 3).....                     | Plants.                                                       |
| 23..... | Near middle of east half.....        | 8       | 5              | 16         | 1,350.....                          | Footprints, plants.                                           |
| 24..... | NW of NW.....                        | 2       | 3              | 15         | 800.....                            | See faunal list.                                              |
| 25..... | SW of SE.....                        | 35      | 4              | 15         | 800.....                            | Do.                                                           |
| 26..... |                                      | 31      | 6              | 16         | LANCE.....                          | (Not relocated.) Plants.                                      |
| 27..... | NE of SE.....                        | 30      | 6              | 15         | 1,750.....                          | See faunal list.                                              |
| 28..... | NW of SW.....                        | 29      | 6              | 15         | 1,750.....                          | Do.                                                           |
| 29..... | NW of NW.....                        | 29      | 6              | 15         | (In No. 2).....                     | Invertebrates.                                                |
| 30..... | NW.....                              | 30      | 6              | 15         | 850.....                            | Champsosaur and mammal fragments.                             |
| 31..... |                                      | 26      | 6              | 15         | LANCE.....                          | (Not relocated.) Invertebrates.                               |
| 32..... |                                      | 25      | 5              | 15         | (In No. 3).....                     | Do.                                                           |
| 33..... | SW.....                              | 17      | 5              | 15         | 2,250.....                          | Invertebrates.                                                |
| 34..... |                                      | 36      | 7              | 16         | KOOTENAI.....                       | (Not relocated.) Plants.                                      |
| 35..... | NE of SE.....                        | 33      | 6              | 16         | (In No. 3).....                     | Plants.                                                       |
| 36..... | Near center of north line.....       | 20      | 5              | 15         | 2,250.....                          | See "Princeton Localities."                                   |
| 37..... | NE of SE.....                        | 33      | 6              | 16         | (In No. 3).....                     | Plants, invertebrates.                                        |
| 38..... | SE of NW.....                        | 17      | 5              | 15         | 2,250.....                          | See "Princeton Localities."                                   |
| 39..... | SE of SE.....                        | 15      | 4              | 15         | 1,350.....                          | See faunal list.                                              |
| 40..... | SW of NW.....                        | 29      | 5              | 15         | 2,300.....                          | See "Princeton Localities."                                   |
| 41..... | SE of NW.....                        | 29      | 5              | 15         | 2,325.....                          | Do.                                                           |
| 42..... | NE of NW.....                        | 20      | 5              | 15         | 2,250.....                          | Do.                                                           |
| 43..... | NW of NW.....                        | 20      | 5              | 15         | 2,250.....                          | Do.                                                           |



TABLE 2.—*Serial list of localities, Crazy Mountain Field, Mont.*—Continued

| No.     | Quarter                            | Section | Town-<br>ship<br>North | Range<br>East | Feet above<br>base of Fort<br>Union No. 1 | Remarks                               |
|---------|------------------------------------|---------|------------------------|---------------|-------------------------------------------|---------------------------------------|
| 44..... | SE of SE.....                      | 7       | 5                      | 15            | 2,500.....                                | See "Princeton Localities."           |
| 45..... | SE of SW of SW.....                | 17      | 5                      | 15            | 2,250.....                                | Do.                                   |
| 46..... | NW of NW.....                      | 24      | 5                      | 14            | (In No. 3)...                             | Invertebrates.                        |
| 47..... | NE of NE.....                      | 10      | 5                      | 14            | (In No. 3)...                             | Plants.                               |
| 48..... | NE.....                            | 25      | 5                      | 14            | (In No. 3)...                             | Do.                                   |
| 49..... | NW of NW.....                      | 23      | 5                      | 14            | 4,350.....                                | Mammal fragments.                     |
| 50..... | Near middle of south<br>half.      | 9       | 3                      | 15            | 800.....                                  | See faunal list.                      |
| 51..... | SW.....                            | 24      | 4                      | 15            | 575.....                                  | Do.                                   |
| 52..... | NW of NE.....                      | 23      | 5                      | 15            | 1,150.....                                | Do.                                   |
| 53..... | NW of NW of NW.....                | 14      | 4                      | 15            | 1,350.....                                | Do.                                   |
| 54..... | NW of NE.....                      | 23      | 5                      | 15            | 1,200.....                                | Do.                                   |
| 55..... | NW.....                            | 29      | 5                      | 15            | 2,300.....                                | Invertebrates.                        |
| 56..... | SE of NW.....                      | 13      | 5                      | 14            | 3,350.....                                | SCARRITT QUARRY.                      |
| 57..... | SW of SE.....                      | 17      | 5                      | 15            | 2,250.....                                | See "Princeton Localities."           |
| 58..... | Near center line in north<br>half. | 20      | 5                      | 15            | 2,250.....                                | Invertebrates.                        |
| 59..... | East half.....                     | 20      | 5                      | 15            | 2,250.....                                | See "Princeton Localities."           |
| 60..... | SE of NW of SW.....                | 19      | 5                      | 15            | 2,275.....                                | Do.                                   |
| 61..... | SE.....                            | 1       | 5                      | 14            | (In No. 3)...                             | Do.                                   |
| 62..... | SW of SW.....                      | 7       | 5                      | 15            | 2,850.....                                | Do.                                   |
| 63..... | NW.....                            | 18      | 5                      | 15            | 2,850.....                                | Do.                                   |
| 64..... | SW.....                            | 34      | 6                      | 16            | 1,250.....                                | Mammal fragments.                     |
| 65..... | SE of SW.....                      | 26      | 6                      | 16            | 35.....                                   | See faunal list.                      |
| 66..... | SW.....                            | 14      | 5                      | 13            | 5,160.....                                | Do.                                   |
| 67..... | SE of SE.....                      | 10      | 5                      | 13            | 5,000.....                                | Plants, invertebrates, rep-<br>tiles. |
| 68..... | Near center of north line.         | 20      | 5                      | 15            | 2,250.....                                | See "Princeton Localities."           |
| 69..... | SW.....                            | 18      | 5                      | 15            | 2,850.....                                | Do.                                   |
| 70..... | Near middle of east half.          | 31      | 6                      | 15            | (In No. 3)...                             | See faunal list.                      |
| 71..... | SE of SE.....                      | 36      | 6                      | 14            | (In No. 3)...                             | Mammal fragments.                     |
| 72..... | Near middle of north<br>half.      | 12      | 5                      | 14            | (In No. 3)...                             | See "Princeton Localities."           |
| 73..... | NE of SW.....                      | 34      | 6                      | 16            | 500.....                                  | See faunal list.                      |
| 74..... | NE of NE.....                      | 15      | 5                      | 15            | 1,350.....                                | Fish.                                 |
| 75..... | SW.....                            | 5       | 4                      | 16            | (Lower part<br>of No. 2).                 | Mammal fragments.                     |
| 76..... | SW of SE.....                      | 11      | 5                      | 15            | (Lower part<br>of No. 2).                 | Do.                                   |
| 77..... | NE.....                            | 32      | 5                      | 15            | (In No. 3)...                             | Do.                                   |
| 78..... | SW of SW.....                      | 26      | 6                      | 16            | 200.....                                  | See faunal list.                      |
| 79..... | NE.....                            | 10      | 5                      | 13            | (High in No.<br>3).                       | Champsosaur.                          |
| 80..... | NE.....                            | 14      | 5                      | 13            | (High in No.<br>3).                       | Plants.                               |
| 81..... | Near middle line in<br>south half. | 23      | 6                      | 15            | 800.....                                  | See faunal list                       |
| 82..... | SW of SW of SW.....                | 11      | 4                      | 15            | 1,350.....                                | Do.                                   |

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## TOWNSHIP 5 NORTH, RANGE 14 EAST

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## TOWNSHIP 6 NORTH, RANGE 14 EAST

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## TOWNSHIP 3 NORTH, RANGE 15 EAST

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## TOWNSHIP 5 NORTH, RANGE 15 EAST

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Section 29: Locs. 40, 41, 55.

Section 17: Locs. 33, 38, 45, 57.

Section 32: Loc. 77.

Section 18: Locs. 63, 69.

## TOWNSHIP 6 NORTH, RANGE 15 EAST

Section 23: Locs. 8, 81.

Section 31: Loc. 70.

Section 26: Loc. 31.

Section 34: Loc. 16.

Section 29: Locs. 28, 29.

Section 35: Loc. 9.

Section 30: Locs. 12, 27, 30.

## TOWNSHIP 4 NORTH, RANGE 16 EAST

Section 5: Loc. 75.

Section 7: Loc. 2.

## TOWNSHIP 5 NORTH, RANGE 16 EAST

Section 4: Loc. 1.

Section 8: Loc. 23.

## TOWNSHIP 6 NORTH, RANGE 16 EAST

Section 25: Loc. 7.

Section 33: Locs. 5, 35, 37.

Section 26: Locs. 65, 78.

Section 34: Locs. 6, 16, 22, 64, 73.

Section 31: Loc. 26.

## TOWNSHIP 7 NORTH, RANGE 16 EAST

Section 36: Loc. 34.





TABLE 3.—Combined faunal list, Crazy Mountain Field, Mont.—Continued

| Species                                                    | No. 1            | No. 2    |          |                  |            | No. 3      |                  |                  |                  |            |
|------------------------------------------------------------|------------------|----------|----------|------------------|------------|------------|------------------|------------------|------------------|------------|
|                                                            | (At level shown) | 575 feet | 800 feet | 1,150-1,200 feet | 1,265 feet | 1,350 feet | 1,700-1,750 feet | 2,250-2,350 feet | 3,350-3,500 feet | 4,350 feet |
|                                                            | <i>Feet</i>      |          |          |                  |            |            |                  |                  |                  |            |
| <i>Myrmecoboides montanensis</i> .....                     |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Stilpnodon simplicidens</i> .....                       |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Bessocetor diluculi</i> .....                           |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Bessocetor thomsoni</i> .....                           |                  |          |          |                  |            |            |                  |                  | X                |            |
| Cf. <i>Palaeosinopa</i> sp.....                            |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Aphronorus fraudator</i> .....                          |                  |          | X        | X                | X          |            |                  |                  |                  |            |
| <i>Eudaemonema cuspidata</i> .....                         |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Elpidophorus patatus</i> .....                          |                  |          |          |                  |            |            |                  |                  | X                | X          |
| <i>Elpidophorus minor</i> .....                            |                  |          |          |                  | X          |            |                  |                  |                  |            |
| <i>Picrodus silbertingi</i> .....                          |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Unuchinia asaphes</i> .....                             |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Pronothodectes matthewi</i> .....                       |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Plesiadapis anceps</i> .....                            |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Plesiadapis rex</i> .....                               |                  |          |          |                  |            |            |                  |                  |                  | X          |
| <i>Elphidotarsius florencae</i> .....                      |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Carpodaptes hazelae</i> .....                           |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Paromomys maturus</i> .....                             |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Paromomys depressidens</i> .....                        |                  |          |          | X                |            |            |                  |                  |                  |            |
| Cf. <i>Paromomys</i> , genus and species undetermined..... |                  |          |          |                  |            |            |                  |                  |                  | X          |
| <i>Palaechthon alticuspis</i> .....                        |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Palenochtha minor</i> .....                             |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Phenacolemur frugivorus</i> .....                       |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Conoryctes comma</i> .....                              |                  |          |          | X                | X          |            |                  |                  |                  |            |
| Cf. <i>Conoryctes</i> sp.....                              |                  |          |          |                  |            |            | X                |                  |                  |            |
| <i>Psittacotherium multifragum</i> .....                   |                  |          |          |                  | X          |            |                  |                  |                  |            |
| <i>Claenodon montanensis</i> .....                         |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Claenodon silbertingi</i> .....                         |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Claenodon latidens</i> .....                            |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Claenodon vecordensis</i> .....                         | 300              |          |          |                  |            |            |                  |                  |                  |            |
| <i>Claenodon ?ferox</i> .....                              |                  |          |          |                  |            | X          |                  | X                |                  | X          |
| <i>Claenodon</i> sp.....                                   |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Deuteronodon montanus</i> .....                         |                  |          | X        |                  |            |            |                  |                  |                  |            |
| ? <i>Deuteronodon</i> sp.....                              |                  |          | X        |                  |            |            |                  |                  |                  |            |
| <i>Prothryptacodon furens</i> .....                        |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Prothryptacodon ?furens</i> .....                       |                  |          | X        |                  |            |            |                  |                  |                  |            |
| <i>Thryptacodon faustralis</i> .....                       |                  |          |          |                  |            |            |                  |                  |                  | X          |
| <i>Chriacus pugnax</i> .....                               | 200              |          |          |                  |            |            |                  |                  |                  |            |
| Cf. <i>Chriacus</i> sp.....                                |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Metachriacus punitor</i> .....                          |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Metachriacus provocator</i> .....                       |                  | X        | X        |                  |            |            |                  |                  |                  |            |
| <i>Metachriacus</i> sp.....                                |                  | X        |          |                  | X          |            |                  |                  |                  |            |
| <i>Spanoxyodon latrunculus</i> .....                       |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Mimotricentes latidens</i> .....                        |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Mimotricentes ?latidens</i> .....                       |                  |          | X        |                  | X          |            |                  |                  |                  |            |
| <i>Mimotricentes angustidens</i> .....                     | 500              | X        |          |                  | X          |            |                  |                  |                  |            |
| ? <i>Mimotricentes</i> sp.....                             | 300              |          |          |                  |            |            |                  |                  |                  |            |
| <i>Didymictis microlestes</i> .....                        |                  |          | X        | X                | X          |            |                  |                  |                  |            |
| <i>Didymictis tenuis</i> .....                             |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Didymictis ?haydenianus</i> .....                       |                  | X        | X        |                  | X          |            |                  |                  |                  |            |
| <i>Ictidopappus mustelinus</i> .....                       |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Dissacus</i> sp.....                                    |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Ellipsodon aquilonius</i> .....                         |                  | X        |          | X                | X          |            |                  |                  |                  |            |
| <i>Ellipsodon</i> sp.....                                  |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Litaletes disjunctus</i> .....                          |                  | X        |          | X                |            |            |                  |                  |                  |            |

TABLE 3.—Combined faunal list, Crazy Mountain Field, Mont.—Continued

| Species                                     | No. 1            | No. 2    |          |                  |            | No. 3      |                  |                  |                  |            |
|---------------------------------------------|------------------|----------|----------|------------------|------------|------------|------------------|------------------|------------------|------------|
|                                             | (At level shown) | 575 feet | 800 feet | 1,150-1,200 feet | 1,265 feet | 1,350 feet | 1,700-1,750 feet | 2,250-2,350 feet | 3,350-3,500 feet | 4,350 feet |
|                                             | <i>Feet</i>      |          |          |                  |            |            |                  |                  |                  |            |
| <i>Litomylus dissentaneus</i> .....         |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Haplaletes disceptatrix</i> .....        |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Cf. Haplaletes</i> sp.....               |                  |          |          |                  |            |            |                  |                  |                  | X          |
| <i>Litolestes notissimus</i> .....          |                  |          |          |                  |            |            |                  |                  | X                |            |
| <i>Tetracraenodon symbolicus</i> .....      |                  |          | X        |                  | X          |            |                  |                  |                  |            |
| <i>Tetracraenodon cf. symbolicus</i> .....  | 300              | X        |          |                  |            |            |                  |                  |                  |            |
| <i>Tetracraenodon cf. puericensis</i> ..... |                  |          |          | X                |            | X          |                  |                  |                  |            |
| <i>Tetracraenodon</i> spp.....              |                  |          |          |                  |            |            |                  |                  | X                | X          |
| <i>Gidleyina montanensis</i> .....          |                  |          |          |                  |            |            |                  | X                |                  |            |
| ? <i>Gidleyina silberlingi</i> .....        |                  |          |          |                  |            |            | X                |                  |                  |            |
| ? <i>Gidleyina superior</i> .....           |                  |          |          |                  |            |            |                  |                  |                  | X          |
| ? <i>Gidleyina</i> sp.....                  |                  |          |          |                  |            |            |                  | X                |                  |            |
| <i>Coriphagus montanus</i> .....            |                  |          |          | X                | X          |            |                  |                  |                  |            |
| <i>Anisonchus sectorius</i> .....           |                  | X        | X        | X                |            |            | X                | X                | X                |            |
| <i>Pantolambda intermedius</i> .....        |                  |          |          | X                |            |            |                  |                  |                  |            |
| ? <i>Pantolambda</i> sp.....                |                  |          |          | X                |            |            |                  |                  |                  |            |
| <i>Pantolambdids</i> undetermined.....      |                  |          |          |                  |            | X          | X                | X                | X                |            |

## FAUNAL SUCCESSION

The No. 1 beds have yielded only ?*Ptilodus sinclairi* from near the base; *Claenodon recordensis*, *Chriacus pugnax*, ?*Mimotricentes* sp., and *Tetracraenodon ?symbolicus* from near the middle part; and *Mimotricentes angustidens* from the top. The first and last of these forms are inseparable from species occurring well up into the No. 2, and so is *Tetracraenodon ?symbolicus*. *Claenodon recordensis* and *Chriacus pugnax* are distinct species but cannot be considered to be clearly ancestral to anything known from the No. 2. The evidence is inadequate to demonstrate either occurrence or absence of distinct faunal advance within the No. 1-No. 2 series. It does suggest, however, that such advance must have been relatively slight and that it was probably of less than generic rank, if it occurred. The data definitely, if not altogether conclusively, oppose the hypothesis that the difference between No. 1 and No. 2 faunas can have been as great as between Puerco and Torrejon.

Within the No. 2 beds the first important point is that the *Gidley* and *Silberling* Quarry faunas are identical in degree of evolutionary progress and show no significant difference in age despite a small difference in level, about 65 feet. There are 23 species definitely identified in the *Silberling* Quarry. Seventeen of these also occur in the *Gidley* Quarry and, as shown in the systematic descriptions, these suggest no difference, even of less than specific rank, between the forms in the two quarries. Four *Silberling* Quarry species do not occur in the *Gidley* Quarry but do occur at lower levels, so that their

absence in the Gidley Quarry is not due to time differences but to facies or accidents of discovery. These species are *Eucosmodon sparsus*,<sup>12</sup> *Mimotricentes angustidens*, *Didymictis haydenianus*,<sup>12</sup> and *Tetraclaenodon symbolicus*. Only two species, *Psittacotherium multifragum* and *Elpidophorus minor*, known only from one specimen each, are confined to the Silberling Quarry, and there can be no doubt that this is the result of chance. The Gidley and Silberling Quarry faunas are, then, a unit as far as appreciable differences in time are concerned.

The 575-foot level is represented by eight definitely identified species, of which seven also occur in the Gidley or Silberling Quarries or both, and the other, *Metachriacus provocator*, reappears at the 800-foot level. The 800-foot localities have 10 definitely identified species, 8 of which also occur in the Gidley or Silberling Quarries or both, while *Deuteronogonodon montanus* is confined to this level and *Metachriacus provocator* appears also 225 feet lower. All the material of *Deuteronogonodon montanus* is from a single locality, and it must be considered as a sporadic and chance occurrence with no probable validity as an index of time relationship, particularly as no probable or possible ancestral or descendent forms occur in this field. The distribution of *Metachriacus provocator* is peculiar. It is relatively very abundant at No. 2 levels below the Gidley Quarry, being the only species that occurs at all these localities (except for Loc. 52, which is only 50 feet below the Gidley Quarry and must be considered as at essentially the same level). At the Gidley and Silberling Quarry levels it has not been found, but an allied species, *M. punitor*, is present and fairly common. *M. provocator* is the larger and in some other respects probably the more specialized of the two species, despite its earlier appearance. Thus the relationship is not that of ancestor to descendant, and no temporal difference is demonstrated. The facies of these earlier localities are demonstrably quite different from those of the quarries, and the most reasonable conclusion is that the distribution of the two species of *Metachriacus* is conditioned by facies and not by time.

It thus appears that the whole Fort Union No. 2 shows no probable significant faunal advance and that it forms a unit as far as time and correlation are concerned.

It is particularly unfortunate that the three lower fossil zones of the No. 3 beds are represented by few and poor specimens, for this is a crucial point in the sequence, probably covering (as shown under "Correlation") the transition from Middle to Upper Paleocene. The lowest level, 1,350 feet, yields *Claenodon ?ferox*, *Tetraclaenodon* cf. *puercensis*, and indeterminable pantolambdids. The latter have no particular importance. *Claenodon ?ferox* occurs almost throughout

<sup>12</sup> These probably are present in unprepared Gidley Quarry material.



the No. 3 beds but is not recorded in the No. 2 where there are smaller and probably somewhat more primitive species of the same genus. The *Tetraclaenodon* is not distinguishable from one in the Gidley Quarry, or from fragmentary specimens from high in the No. 3. The 1,700-foot level has cf. *Conoryctes* sp., *Gidleyina silberlingi*, *Anisonchus sectorius*, and pantolambdids. The first and last have no apparent significance for this discussion. *Gidleyina silberlingi* marks the first (probable) appearance of that genus, which seems to be confined to the No. 3 and more progressive than anything in the No. 2. *Anisonchus sectorius* ranges throughout the No. 2 and far up into the No. 3.

The 2,250 to 2,350 levels (chiefly "Princeton localities") yield *Claenodon ?ferox*, *Gidleyina montanensis* and *G.* spp., *Anisonchus sectorius*, and pantolambdids that are undetermined but are distinct from anything in the No. 2 beds. Loc. 15, which is somewhere in the lower No. 3 although not determined exactly as to level, yields an ally of *Paromomys* not demonstrably distinct from the No. 2 representation of that group.

These lower No. 3 beds as a whole appear to be characterized by the survival of some genera, including *Claenodon*, *Tetraclaenodon*, *Anisonchus*, and perhaps *Paromomys* and *Conoryctes*, and of at least one species, *Anisonchus sectorius*, from the No. 2 beds, and by the appearance of a distinctive advanced species, *Claenodon ?ferox*, and a similarly distinctive and relatively specialized genus, *Gidleyina*. These two latter may not be real cases of faunal advance, for it is possible that these animals were already present in No. 2 time despite the lack of discovery, yet it seems tentatively acceptable to consider them as suggestive of some slight faunal progress. The data are too scanty for any definitive conclusion, but the indications are that these strata have a transitional fauna between that of the No. 2 beds and that of the Scarritt Quarry, about 1,000 feet above these lower No. 3 levels.

The Scarritt Quarry, at about 3,350 feet, provides good data and for the first time shows decisive and incontrovertible evidence of faunal change in the series. *Ectypodus hunteri* is evidently related to some species from the Gidley Quarry but is certainly distinct and probably of later aspect, and the same is true of *Leptacodon* cf. *tener*. *Bessoecetor thomsoni* also has a Gidley Quarry ally but is probably not a descendant of the latter. The relative degree of specialization is not clear. *Elpidophorus pat ratus* is more specialized than its fore-runner *?E. minor* in the Silberling Quarry. *Plesiadapis anceps* is very primitive in its genus yet is more advanced than *Pronothodectes*, from which it could well have been derived. The relation between *Carpodaptes* in the Scarritt Quarry and *Elphidotarsius* in the Gidley Quarry is closely analogous to that between *Plesiadapis* and *Pronothodectes*. *Phenacolemur* has no definitely recognizable ancestor in the

lower beds but is a progressive and specialized form. *Litolestes* is allied to *Haplaletes* and might have been, but probably was not, derived from the latter (but surely not from the known species). In any case, it is a distinctive genus abundant here and unknown in the No. 2 beds. *Tetraclaenodon* occurs in both series, and the species are not well enough known for useful comparison. Finally, *Anisonchus sectorius*, which ranges throughout the No. 2, is also present here (not in the Scarritt Quarry but at Loc. 18, which is not appreciably different in level).

If we discount the influence of facies and chance as far as possible, it then seems clear that there is definite faunal advance from the Gidley and Silberling Quarry levels to that of the Scarritt Quarry, that this advance is in some cases of generic rank (*Pronothodectes-Plesiadapis* and *Elphidotarsius-Carpodaptes*) but in others only specific (probably in the genera *Ectypodus*, *Leptacodon*, *Bessoeceptor*, *Elpidophorus*, and *Tetraclaenodon*) and in part of even less degree (*Anisonchus sectorius*).<sup>13</sup>

The progressive difference in the two faunas compared is real, but it is not very marked, much less than would be expected from a difference in level of some 2,000 feet. As nearly as such an imperfect parallel can be drawn, the difference seems to be definitely less than that between the Torrejon and the Tiffany and probably not much greater than between the Tiffany and Clark Fork.

The highest faunal level, 4,350 feet, has provided little good evidence bearing on this discussion. *Plesiadapis rex* may be more progressive than *P. anceps* but is not definitely shown to be so. The *Paromomys*-like form is too poorly known for useful comparison. *Tetraclaenodon* still occurs at the higher level and so probably does *Gidleyina*, their degree of advance, if any, over comparable forms lower in the No. 3 beds not being clear.

*Claenodon ?ferox* still occurs here and seems to be quite as in the lower No. 3, although the material is scanty. *Thryptacodon*, identified with much probability but not certainty, is progressive over *Prothryptacodon* of the No. 2, but the intermediate stages in the lower No. 3 are unknown. An ally of *Haplaletes* here is too poorly known to give reliable evidence. *Elpidophorus*, probably *patratus*, carries through from the Scarritt Quarry level. The data are too inadequate to say that there is no advance over the Scarritt Quarry, or indeed over the lower No. 3, but they suggest that the difference will probably prove to be slight if it exists at all.

<sup>13</sup> The tremendous vertical range of *Anisonchus sectorius* in this field, nearly 3,000 feet, is extraordinary. This species and to still greater degree this genus are of unusually wide geographic range in the Paleocene, the species known from New Mexico to Montana and the genus also in Louisiana, and also are unusually conservative—the genus is one of the two or three that pass through from Puerco to Torrejon in New Mexico.

## CORRELATION OF MAMMALIAN FAUNAS

Data are not at hand for any exact correlation of the No. 1 beds. Of their mammals ?*Ptilodus sinclairi*, identified here with some probability, is a No. 2 species. *Claenodon* is typically a Middle Paleocene genus, ranging in this field into the Upper Paleocene. *Chriacus* is a very long-lived genus, Lower Paleocene to Lower Eocene, and is here rather dubious but apparently of more progressive aspect than its Lower Paleocene allies. *Mimotricentes* is otherwise known only in the Middle Paleocene of this field, and *M. angustidens* (which, however, is known only from the highest No. 1 beds) ranges to the top of the No. 2. *Tetraclaenodon* is typically Middle Paleocene, perhaps ranging into earliest Upper Paleocene in this field, and the species may be the same as in the No. 2. As identified by Russell (personal communication), invertebrates from immediately below the No. 1 beds, or perhaps in their base, are definitely of Paleocene aspect, and most of his comparisons are closely with Middle to Upper Paleocene forms. On the whole the scanty evidence favors reference of the No. 1 beds to the Middle Paleocene, and none of it definitely suggests or warrants reference to the Lower Paleocene. The physical stratigraphic evidence, while even less decisive, is also consistent with belief that the No. 1 beds are not markedly different from the No. 2 in age. Nothing suggests or justifies correlation with the Puerco.

As already shown, the fauna of the No. 2 beds is a unit as far as correlation is concerned. From his first discovery (Locs. 5 and 6), Douglass (1902) already recognized equivalence to the Torrejon. Matthew (1914) accepted this fauna as of the same age as that of the Torrejon.<sup>14</sup> Gidley (1909, p. 616, footnote, apparently not elsewhere explicitly stated, but his definitive opinion) considered it "about equivalent to . . . or perhaps somewhat older than the Torrejon." The detailed evidence of the mammalian fauna is as follows:

*Ptilodus*: A Middle Paleocene genus, *P. montanus* very near *P. mediaevus* of the Torrejon.

*Ectypodus* } [Typically Upper Paleocene genera, but species here quite distinct-  
*Parectypodus*] } tive and generic assignments not certain.

*Eucosmodon*: Forms indistinguishable generically on the basis of similar material range through the Paleocene.

*Gelastops*: Probably allied to, but distinct from, *Didelphodus* of the Lower Eocene. Probably allied to but less specialized than *Acmeodon* of the Torrejon.

*Prodiacodon*: Middle Paleocene genus, identification here not certain and species highly distinctive.

*Leptacodon*: Genus otherwise Upper Paleocene, species distinctive.

*Myrmecoboides*: Unknown elsewhere, no value in close correlation.

*Stilpnodon*: This genus and its family too imperfectly known for close comparisons.

*Bessoecctor*: Otherwise known only in the No. 3 beds in this field, allied to the typically Lower Eocene *Palaeosinopa*, but more primitive.

<sup>14</sup> His correlation chart, fig. 2, seems to correlate it with the Puerco, but his text shows that this was not intended.



*Aphronorus*: Allied to *Pentacodon* of the Torrejon but apparently more primitive.  
*Eudaemonema*: Allied to *Mixodectes* in the Torrejon and (perhaps more distantly) to other genera in Upper Paleocene and Lower Eocene, more primitive than any of these allies in some respects, but not on the same line of descent as any of them.

*Elpidophorus*: An Upper Paleocene genus but here with a distinctive primitive species, which may well prove generically separable.

*Picrodus*: Probably allied to *Zanycteris* of the Upper Paleocene, relative degree of specialization not determinable.

*Pronothodectes*: Allied to *Plesiadapis* of the Upper Paleocene but distinctly more primitive.

*Elphidotarsius*: Allied to *Carpodaptes* and *Carpolestes* of the Upper Paleocene but distinctly more primitive than either.

*Paromomys*  
*Palaechthon*  
*Palenochtha* } { Generally primitive genera, but exact lines of descent not clear enough for more precise use in correlation.

*Conoryctes*: Genus otherwise Middle Paleocene as far as definitely known, species imperfectly represented but indistinguishable from *C. comma* of the Torrejon.

*Psittacotherium*: Genus otherwise certainly known only in Middle Paleocene, species indistinguishable from *P. multifragum* of the Torrejon.

*Claenodon*: Genus otherwise chiefly Middle Paleocene but extending into Upper Paleocene in this field, species more primitive than that commonest in Torrejon, more comparable to but perhaps slightly more primitive than the second Torrejon species.

*Deuteronogonodon*: A distinctive genus not known elsewhere, perhaps especially allied to, but if so distinctly more advanced than, *Protagonodon* of the Puerco.

*Prothryptacodon*: Allied to *Thryptacodon*, Upper Paleocene and Lower Eocene, but more primitive.

*Metachriacus*  
*Spanoxyodon* } { Genera unknown elsewhere, of Paleocene aspect but not more closely useful in correlation.

*Mimotricentes*: Perhaps especially allied to *Tricentes*, Middle Paleocene, and if so slightly more primitive, but probably on a different line of descent.

*Didymictis*: Genus Middle Paleocene to Lower Eocene, relationship of two species not clear enough for more exact correlation, but a third indistinguishable from *D. haydenianus* of the Torrejon.

*Ictidopappus*: Unknown elsewhere, perhaps especially allied to *Viverravus* of the Eocene, but if so more primitive.

*Dissacus*: Genus Middle Paleocene to Lower Eocene, species not identifiable.

*Ellipsodon*: Genus otherwise only positively identified in Middle Eocene, species close to *E. acolytus*, Torrejon, perhaps slightly more advanced or on different line of descent.

*Litaletes*  
*Litomylus*  
*Haplaletes* } { Genera unknown elsewhere, general aspect Paleocene, perhaps rather more Middle Paleocene, but not exactly determinable as to evolutionary position.

*Tetraclaenodon*: Genus typically Middle Paleocene, probably reaching Upper Paleocene in this field, two species close to those from Torrejon, one of them indistinguishable.

*Coriphagus*: Genus otherwise only in Torrejon, species closely allied.

*Anisonchus*: Genus Lower and Middle Paleocene, also Upper Paleocene in this field only, species same as in Torrejon, but probably also reaches Upper Paleocene here.

*Pantolambda*: Genus certainly identified only in Middle Paleocene, species allied to those of Torrejon.

In résumé, there are 13 genera all of Paleocene aspect but confined to this fauna and of little use in exact correlation. Of the eight other genera confined to this fauna, four have their closest allies in the Torrejon and four have their closest known allies in the Upper Paleocene, but three of these here appear to be distinctly more primitive than their Upper Paleocene relatives. Eight genera are otherwise typical of the Torrejon, and these here include two species indistinguishable from those of the Torrejon. The other species of these genera are in most cases closely allied to those of the Torrejon, mostly without definite evidence of being more or less advanced, but one may be less and one may be more specialized than the most comparable Torrejon species. Four genera are common to this fauna and to that of the Torrejon, but they also appear in later beds. Their species are here generally closer to the Torrejon species and in two cases appear to be identical. Two genera probably range nearly or quite throughout the Paleocene, one of them here represented by a typically Torrejon species, but one that does range into somewhat later beds. Five of the genera are otherwise known only in Upper Paleocene (in some cases also ranging into later) beds, but in each case the species here present is decidedly distinctive, and in no case is a Middle Paleocene ancestor or close ally otherwise known.

This evidence conclusively proves the fauna to belong to the Middle Paleocene and to be close to the Torrejon in age. It does not preclude a slight difference in age from the Torrejon, but differences of facies and geographic position are adequate to explain the faunal distinction without supposing the age to be different, and if the age is slightly different they obscure the evidence for this. There is nothing suggestive of the Puerco. There is a greater resemblance to the Upper Paleocene than is shown by the Torrejon fauna, but the evidence suggests that this is largely or wholly due to the discovery in this place and facies of forerunners of later groups not themselves really later here than the Torrejon.

The only other very closely correlatable horizon is that of the Scarritt Quarry. The correlation has been discussed elsewhere (Simpson, 1936b), where it was shown that the quarry fauna itself is very close to that of the Tiffany in age but may be slightly earlier. From a more general point of view, there is some suggestive but inconclusive evidence strengthening the probability of slightly earlier age for this than for the principal Tiffany horizon. The probable occurrence of *Tetraclaenodon* at an even higher level, replaced in the Tiffany and all later beds by the more advanced and possibly descendant genus *Phenacodus*, weights the evidence in this direction, as does also the occurrence at about this level of a specimen indistinguishable from *Anisonchus sectorius*, a Torrejon species. The occurrence of *Claenodon* indistinguishable from the Torrejon *C. ferox*

far up into the No. 3, even higher than the Scarritt Quarry, is less dependable but suggests the same conclusion. It is also suggestive that the age difference between the Gidley and Silberling Quarry faunas, which are very close to the Torrejon in age, and that of the Scarritt Quarry appears to be less pronounced than the age difference between the Torrejon and the Tiffany.

The Scarritt Quarry and equivalent levels may be correlated with the Tiffany, with the reservation that it is possibly a little earlier, and may be placed in the earliest Upper Paleocene. The highest faunal level, that of Locs. 11 and 13, is likewise surely Upper Paleocene, probably about Tiffany.

The lower levels in the No. 3 cannot be well correlated on present data. They are bounded by Torrejon and (probably early) Tiffany equivalents. There is some slight evidence that they are in fact transitional between these two and represent most of the gap in time known to exist between Torrejon and Tiffany, rather than being more definitely associated with one or the other. If there is a distinct faunal break in this series, it would be logical to look for it at the most obvious change in sedimentation, at the base of the No. 3. The scanty fossil evidence does not warrant such a positive conclusion. The only known elements in the basal No. 3 that look toward the later faunules are *Claenodon ?ferox* of little or no value, since this is, in fact, a typical Torrejon species, and *Gidleyina*, which is more suggestive but in itself far from conclusive.

|            | COLORADO-NEW<br>MEXICO:<br>San Juan Basin | WYOMING:<br>Bighorn Basin                               | MONTANA:<br>Crazy Mountain Field |
|------------|-------------------------------------------|---------------------------------------------------------|----------------------------------|
| PALEOCENE  | (No mammals known)                        | Clark Fork                                              | (No mammals known)               |
|            | Tiffany                                   | "Tiffany-Bear Creek"<br>(Princeton Quarry) <sup>1</sup> | ?                                |
|            | (Faunal break)                            | (Faunal break)                                          | )Scarritt Quarry Melville<br>?)  |
|            | Torrejon                                  | "Torrejon" <sup>1</sup>                                 | Gidley Lebo<br>)Quarry           |
|            | (Faunal break)                            | (Faunal break)                                          | ?                                |
|            | Puerco                                    | "Puerco" <sup>1</sup>                                   | Bear<br>(Age uncertain)          |
| CRETACEOUS | (Unconformity)                            | Lance                                                   | Hell Creek                       |

<sup>1</sup> Dr. Jepsen has not yet applied valid stratigraphic names to these levels, distinguished by him.



The known faunas of this field thus seem to cover most of or all the Middle Paleocene and to continue, probably without a marked break, into the early Upper Paleocene. There are here at least 2,000 feet of sediments of about the same type above the highest level with identified mammals, and sediments of somewhat different character in contiguous areas might raise this figure to as much as 4,000 feet. These beds doubtless represent most of or all the considerable span of later Upper Paleocene time not represented by faunas here, and they may well run into the true Eocene.

The tentative arrangement based on these correlations is summed up in the diagram on page 55.

Such a chart is necessarily excessively simplified, so that it does not adequately represent abundant and exact evidence where this is available; at the same time it must be explicit, so that in places it does not reveal the extent of uncertainty and lack of evidence. It is a correlation of strata by their known faunas, never entirely coextensive with the strata themselves. The "faunal breaks" listed definitely imply intervals of time not represented by known faunas, but it does not follow that strata of these ages are necessarily lacking in the region in question. The same is true of the parts outside the known distribution of faunas that are labeled "no mammals known."

## ECOLOGY

### NOTES ON THE NONMAMMALIAN BIOTA

Despite the abundance of nonmammalian fossils in the field and the existence of good collections made by Silberling and others, this part of the biota has not been adequately studied for this area. It is beyond the scope of the present work to include any critical examination of the material or to attempt complete floral and faunal lists, nor has it seemed necessary to delay publication until such special studies could be made. In the present section a few previous records are mentioned, and beyond this the only purpose is to suggest the broad outlines or general character of the biotic background of the mammalian faunas.

*Plants.*—A number of small collections of leaves have been made in this field, but as far as I know no attempt to collect and to classify its whole flora has been made. Knowlton (1902) has published a special note on one small collection, and several other species are listed incidentally in the literature.

Knowlton (1909, p. 194) listed a few plants from the "lower member of the Fort Union" (by which he usually means the Hell Creek or Lance), 1,000 feet below the top. As it is not clear what he considered "the top", this is not explicit. He states that they were "about 1,200 feet below the small mammals now being studied by Mr. Gidley", which probably means the Silberling Quarry and would (by my esti-

mate) place the plants near the top of the Bear. They are said to be from sec. 29, T. 6 N., R. 16 E., a section that is mainly on the Bear but includes a small area of No. 1. The identifications are:

|                                 |                                    |
|---------------------------------|------------------------------------|
| <i>Salix</i> sp.                | <i>Aralia notata</i> .             |
| <i>Populus amblyrhyncha</i> .   | <i>Leguminosites arachioides</i> . |
| <i>Populus cuneata</i> .        | <i>Vitis xantholithensis</i> .     |
| <i>Populus genetriz</i> .       | <i>Credneria daturaefolia</i> .    |
| <i>Populus daphnogenoides</i> . | <i>Phyllites cupanoides</i> .      |
| <i>Populus</i> sp.              | <i>Carpites</i> sp.                |

These are all common Fort Union species. Knowlton has also reported them all as Lance (e. g., Knowlton, 1919), but on examining the evidence it is found that *Vitis* (or *Ampelopsis*) *xantholithensis*, *Credneria daturaefolia*, and *Phyllites* (or *Pterospermites*) *cupanoides* are true Fort Union species reported in the Lance *only* on the strength of this occurrence, and that there is also some question as to whether *Aralia notata* really occurs in the Cretaceous, whereas it is abundantly characteristic of the Fort Union.<sup>15</sup> In short, this is a Fort Union flora, which would be expected since it is probably from the Bear, which may well be Paleocene or even properly Fort Union, or possibly from the Lebo, which everyone now agrees to be Fort Union.

Other small collections more definitely from the Bear and older than any of the known mammals of this field are mentioned above.

A collection surely from the Lebo, "close under the massive gray sandstone of the Fort Union" (i. e., the base of the No. 3 beds), in "Sec. 15, T. 6 N., R. 15 E." (actually sec. 22, as later surveys have shown; sec. 15 includes only the very base of the Lebo), was made by Campbell, Stanton, Stone, and Calvert, and identified by Knowlton as follows (in Stone and Calvert, 1910, p. 755):

|                               |                                  |
|-------------------------------|----------------------------------|
| <i>Platanus haydenii</i> .    | <i>Sapindus grandifoliolus</i> . |
| <i>Populus cuneata</i> .      | <i>Grewia obovata</i> .          |
| <i>Populus amblyrhyncha</i> . | <i>Grewiopsis platanifolia</i> . |

These are all Fort Union species, and all occur in the Glendive region. The majority also occur in the Lance but are certainly in the Fort Union in this section.

Knowlton (1902) described a small flora collected by W. H. Weed from "the sandstone series above the bend of the Sweet Grass, west of Porcupine Butte, Montana." This locality is in this field, at the extreme western edge of the mapped area, at a high horizon, far above any identified mammals. The following species were recorded: *Glyptostrobus europaeus*,<sup>16</sup> *Onoclea sensibilis fossilis*, *Aralia ?notata*, and *Tilia weedii*. The last has not been recorded elsewhere, but the others are Fort Union (and questionably earlier) species, and Knowl-

<sup>15</sup> This incident casts further doubt on the supposed community of the Lance and Fort Union floras, for there are many other areas where beds probably or surely Paleocene and definitely post-Hell Creek have been arbitrarily called "Lance."

<sup>16</sup> *G. e. ungeri* in the original list, but later emended by Knowlton to the form here given.

ton concludes that the beds are Fort Union. Incidentally this is some slight evidence that these upper beds are still in the Paleocene, but this perhaps cannot be taken very seriously.

It seems probable that the Fort Union flora of this field is closely similar to that of the Bull Mountain field (lists in Woolsey, Richards, and Lupton, 1917) and also to the very large and well-known flora of the Glendive area (lists and references in Knowlton, 1919), in short, that it is the typical, wide-ranging Fort Union flora, which seems to have shown little geographic or stratigraphic differentiation from Upper Cretaceous to Upper Paleocene and throughout the West. Leaves are found at almost all levels and throughout the field, although really well-preserved specimens can seldom be recovered. Specimens apparently of the handsome species *Platanus nobilis* were particularly noticeable in the sandstones stripped from above the bone layer in the Gidley Quarry. The general occurrence of leaves here and elsewhere in the field suggests that the whole region was heavily forested, chiefly by deciduous trees, during much of or all the Paleocene. It demonstrates the presence of a well-developed arboreal habitat and of abundant food for browsing and frugivorous animals and suggests (but by no means proves) that the more open type of plains habitat was here relatively restricted or absent.

Knowlton (1927, pp. 184-186) has summed up the Fort Union flora in general, and probably his remarks apply in large measure to the plants of this field throughout Lebo and Melville time. About a dozen species of small ferns and the sensitive fern *Onoclea* are known, as well as horsetails, "a beautiful little selaginella", and abundant grasses and sedges. Only one palm, and that rare, is recorded. "It was, however, a very large-leaved fan-palm, showing that conditions were not altogether unfavorable." Conifers are abundant, with three sequoias, a yew, bald cypress, two or three pines, and an arbovitae that was particularly abundant. There is a rare ginkgo. The most conspicuous and abundant dicotyledonous trees were poplars, with leaves suggestive of the quaking aspen. Sycamores also were abundant, some with very large leaves. Viburnums were also very common and were "presumably small trees or shrubs, known at the present day as arrowwood, blackhaw, tree cranberry, etc." There were also oak, alder, chestnut, hazelnut, maple, elm, magnolia, hickory, walnut, birch, beech, ampelopsis, bittersweet, and rare figs and laurels.

*Invertebrates*.—Mollusks occur throughout the field and often in extraordinary abundance. The majority of them are fresh-water mussels and gastropods, although a few may be terrestrial snails. The common types are several different species each of "*Unio*", *Viviparus*, and *Campeloma*. A large collection from just below the Lebo has been listed page 17. Dr. Russell has also identified the



following from Loc. 24 (immediately above the mammals): *Viviparus retusus*, *V. planolatre*, and *Lioplax nebrascensis*; and the following from Loc. 67, high in the No. 3: ?*Nedionidus senectus*, ?*N. s. declivis* (type locality; Russell, 1934), *Viviparus retusus*, and *V. cf. planolatre*.

(There are also large collections not adequately studied, nor is it necessary to discuss them here where only the general ecological aspect is in question.)

Altogether, the invertebrates show that fresh water was abundantly present and thickly populated in this area throughout the deposition of the Fort Union.

*Fishes*.—Fish remains are abundant in the field but usually very fragmentary. A few relatively good specimens have been recovered but have not yet been prepared or closely studied. Gar scales (*Lepisosteus* sp.) are common at most surface localities and also occur in all three quarries. A still commoner fish in the quarries, seldom found on surface exposures, probably because of its more fragile character, appears to be an ally of, or to belong to, *Stylomyledon* Russell, and Russell has already recorded its presence in this field (1928, p. 107). Specimens recently collected will add greatly to knowledge of this form. Despite the almost complete lack of association of mammal remains in the Gidley Quarry, it is the rule rather than the exception to find fishes, apparently mostly *Stylomyledon*, represented by associated strings of vertebrae, despite the loose articulation of these, and not infrequently also with parts of the skull in association.

*Reptiles*.—Champsosaur and crocodilian remains, generally too imperfect for close identification, are common at all levels. Isolated teeth suggest that *Allognathosuchus* was the common crocodilian. Champsosaurs occur up to at least 3,000 feet, and possibly more, above the base of the No. 3. Turtle remains are also common, but they also are usually too fragmentary for ready identification. Hay (1908, p. 498) has, however, described *Aspideretes nassau* from a specimen found by one of the Princeton parties in the No. 3 beds.

Gilmore (1928b) has mentioned three fragmentary specimens of *Peltosaurus* sp. from the Fort Union No. 2 Silberling Quarry and has also named *Harpagosaurus excedens*, the type of which is from the same locality. Lizard remains are fairly common in both Silberling and Gidley Quarries, and it is probable that these animals were abundant in this region in the Middle Paleocene.

#### MAMMALIAN FACIES

The percentage composition of the principal No. 2 surface localities, all near the same level and similar in facies, and of each of the three quarries is given in table 4 and shown graphically in figures 1 and 2.

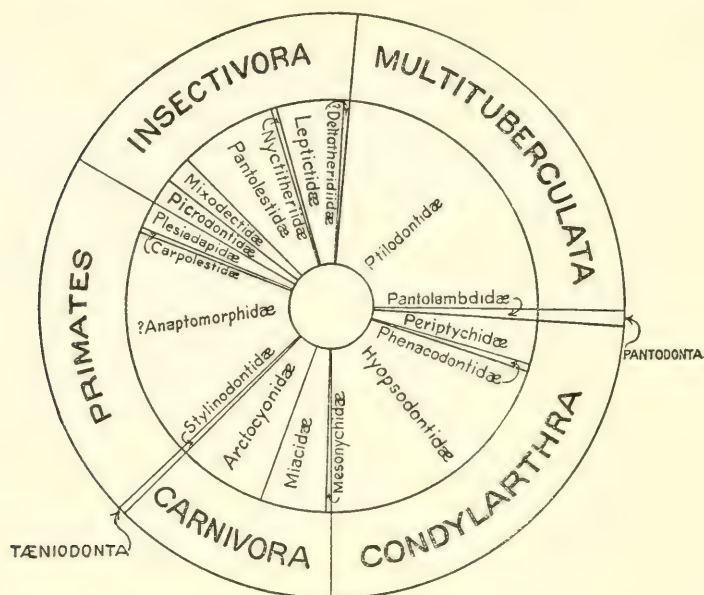
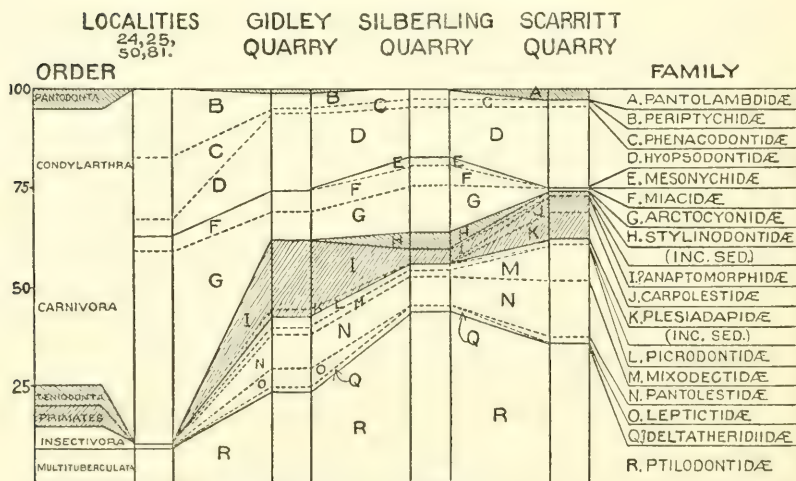


FIGURE 1.—Diagram showing the relative abundance of identified individuals of the various orders and families of mammals in the National Museum collection from the Gidley Quarry.



(P. NYCTITHERIIDÆ IN GIDLEY QUARRY LESS THAN ¼ PER CENT.)

FIGURE 2.—Comparison of relative abundance of families of mammals at various localities in the Crazy Mountain Field, Mont. Abundance is indicated for each locality by percentages of identified individuals in the National Museum collection. Four Lebo surface localities (combined) and the three principal quarries are compared.

TABLE 4.—*Composition (in percentages) of the principal No. 2 surface localities and of each of the three quarries, Crazy Mountain Field, Mont.*

| Order and family       | Localities<br>51, 24, 25,<br>50, and 81. | Gidley<br>Quarry | Silberling<br>Quarry | Scarritt<br>Quarry |
|------------------------|------------------------------------------|------------------|----------------------|--------------------|
| MULTITUBERCLATA:       | 9                                        | 24               | 44                   | 36                 |
| Ptilodontidae.....     | 9                                        | 24               | 44                   | 36                 |
| INSECTIVORA:           | 1                                        | 18               | 12                   | 26                 |
| ?Deltatheridiidae..... | 0                                        | 1                | 2                    | 0                  |
| Leptictidae.....       | 0                                        | 5                | 0                    | 1                  |
| Nyctitheriidae.....    | 0                                        | (1)              | 0                    | 0                  |
| Pantolestidae.....     | 1                                        | 8                | 7                    | 15                 |
| Mixodectidae.....      | 0                                        | 2                | 2                    | 9                  |
| Picrodontidae.....     | 0                                        | 2                | 2                    | 0                  |
| Incertae sedis.....    | 0                                        | 0                | 0                    | 1                  |
| PRIMATES:              | 0                                        | 20               | 4                    | 13                 |
| Plesiadapidae.....     | 0                                        | 2                | 0                    | 7                  |
| Carpolestidae.....     | 0                                        | (1)              | 0                    | 4                  |
| ?Anaptomorphidae.....  | 0                                        | 18               | 4                    | 0                  |
| Incertae sedis.....    | 0                                        | 0                | 0                    | 1                  |
| TAENIODONTA:           | 0                                        | (1)              | 4                    | 0                  |
| Stylinodontidae.....   | 0                                        | (1)              | 4                    | 0                  |
| CARNIVORA:             | 53                                       | 13               | 19                   | 1                  |
| Arctocyonidae.....     | 49                                       | 7                | 12                   | 1                  |
| Miacidae.....          | 4                                        | 5                | 5                    | 0                  |
| Mesonychidae.....      | 0                                        | (1)              | 2                    | 0                  |
| CONDYLARTHRA:          | 37                                       | 24               | 18                   | 22                 |
| Hyopsodontidae.....    | 4                                        | 20               | 14                   | 21                 |
| Phenacodontidae.....   | 16                                       | 1                | 2                    | 1                  |
| Periptychidae.....     | 16                                       | 4                | 2                    | 0                  |
| PANTODONTA:            | 0                                        | 1                | 0                    | 2                  |
| Pantolambdidae.....    | 0                                        | 1                | 0                    | 2                  |

<sup>1</sup> Represented by 1 specimen (less than 0.5 percent).

The figures represent the composition of the identified collections. They are somewhat biased in favor of the multituberculates, since practically all the specimens of these are identified, whereas there are numerous isolated teeth of other orders that are not identified, but in general they are representative of the faunas as they occur.

The Gidley and Silberling Quarries agree well, within the probable limits of chance, except for the much smaller proportion of primates and greater of multituberculates in the Silberling Quarry, a difference probably representing slight local facial distinction.

The surface localities differ remarkably from the quarries and suggest very different environmental conditions. This result is doubtless somewhat biased by the fact that minute forms, like insectivores and primates, are more likely to break up and are harder to find at surface localities, but this does not explain the difference. Some of the so-called surface material was, in fact, found in place. These locali-



ties have been very closely examined and fragments as small as the smallest isolated insectivore or primate teeth recovered, so that the almost total absence of those groups must really result from their great rarity here. Furthermore, the aretocyonids are really much more abundant at these localities, for not only the relative but also the absolute number of specimens is greater for these localities than for the Gidley and Silberling Quarries, despite the much larger collections from the latter. This "surface" fauna, 90 percent carnivores and ungulates, is of more normal type, in comparison with Tertiary faunas generally, than are the quarry faunas. Its members average larger than do those of the quarry faunas, and they are probably terrestrial for the most part. This appears to be a normal flood-plain facies, rather closely analogous to that of the Torrejon.<sup>17</sup> Its most marked peculiarity is the higher percentage of carnivores than of herbivores, a condition for which no probable explanation is seen.

Even at the surface localities there is a surprisingly low percentage of animals really of large size for the Paleocene. The phenacodonts are of average size for that group, but the periptychids (all *Anisonchus*) are moderate in size, much smaller than the contemporaneous *Periptychus*, and most of the carnivores are also of middle size, with *Deuteronodon* very rare and other large carnivores absent, although they were common at this time in the Torrejon.

This rarity of large animals is still more obvious in the quarries. Phenacodonts and pantolambdids are relatively very rare, *Claenodon* is uncommon, and other large mammals do not occur. The most abundant species, *Ptilodus montanus*, ?*P. sinclairi*, *Leptacodon ladae*, *Aphronorus fraudator*, *Paromomys maturus*, *Palaechthon alticuspis*, *Metachriacus punitor*, *Didymictis microlestes*, and *Ellipsodon aquilonius*, are moderate to minute in size.

In food habits the multituberculates were rodentlike, the insectivores doubtless insectivorous (as the word is usually used, not signifying a diet composed of insects), the primates probably mainly or exclusively frugivorous, the creodonts in part omnivorous (*Claenodon*), omnivorous-carnivorous (other aretocyonids), and predaceous-carnivorous (miacids), and the condylarths probably browsing, perhaps in part frugivorous, or even partly insectivorous for the smallest forms. The known fauna apparently consumed every type of food known to have been present in the area, with the possible exception of the mollusks.

The skeletal structure is too poorly known for any of these animals to give much direct insight into their locomotion or general habitus. By analogy and comparison with allied species and genera, the multituberculates and insectivores were unguiculate and probably in good

<sup>17</sup> Correlation of faunal types and collecting methods is real but indirect. Flood-plain deposition and facies would not normally result in concentration of fossils sufficient to permit profitable quarrying.

part arboreal in habitus. The primates, also, may well have been mainly or entirely arboreal. The creodonts were probably mainly terrestrial, but it is probable that some of them were at least semi-arboreal. The abundant hyopsodontids were probably, judged from Torrejon and later allies, more unguiculate than ungulate in general habitus, and the smaller forms may well have been arboreal. The less common larger condylarths and the very rare pantodonts were probably terrestrial. The evidence is not at all conclusive, but it warrants the tentative conclusion that this fauna is largely arboreal, which is well in accord with the evidence that the quarries were in a swampy and heavily forested area and would go far toward explaining the unusual facies of the quarry faunas. There is, indeed, a decidedly fossorial humerus (of unknown association with teeth) in the collection; the facies association of arboreal and fossorial animals is not uncommon and is in accord with a forest environment.

The ordinal composition of the Scarritt Quarry collection differs significantly from that of the Gidley Quarry only in the almost complete absence of carnivores. Within the other orders, the family composition is as nearly similar as would be expected in deposits of similar facies but different ages except among the Primates. The abundant Gidley Quarry types, *Paromomys* and its closer allies, are not represented in the Scarritt Quarry collection, and instead of them the more specialized, perhaps more strictly frugivorous, plesiadapids and carpolestids have become fairly common, although the first were uncommon and the latter very rare in the Gidley Quarry.

The Gidley Quarry is also interesting from the unusual occurrence of its fossils and the indications of the possible conditions surrounding death and burial of its animals. The remains are invariably fragmentary, and with extremely rare exceptions there is no association of specimens. The bones seldom show any signs of weathering or rolling but are usually fractured, and even when they abut against wholly undisturbed matrix these fractures are clean, fresh breaks. Some further fracturing and dissociation have resulted from the compacting of the bed and development of slip planes, but for the most part these preceded fossilization. Most of the jaws have lost some teeth before burial, and many have lost all the teeth. These isolated teeth (clearly lost after death but before burial) are common in the collection. There are many bone fragments, but it is clear that the quantity of skeletal material present, even in the most fragmentary state, cannot by any means represent all the bones of the animals represented by their jaws and teeth.

The rather abundant presence of fish remains, often in articulation, and of aquatic reptile fragments and the presence of aquatic mollusks (rare in this quarry, but present), together with the nature of the sediments, suggest that the deposit was formed in sluggish water, perhaps a

swampy stream course, ox-bow lake, or bayou. From the great variety of mammals present this evidently was not the site of a single or selective catastrophe, like many quarries that seem to represent quicksand or quagmire traps, but must have made a fairly complete sample of the mammals of the surrounding forest and (to a less extent) glades. Regardless of whether the mammals came here to drink, swam into the water, dropped from trees, or were occasionally washed in, it seems likely that the breaking and scattering of their bones, and perhaps commonly their deaths also, were the result of activities of the carnivorous fishes and reptiles. Such a history would probably explain the small ratio of bones to teeth (the former eaten and digested and comminuted, the latter less palatable and more resistant), the many clean breaks, lack of association, and also the common intervention of maceration, without apparent weathering (perhaps in part digestive, and otherwise subaqueous) between death and burial.

#### THE GIDLEY QUARRY AND ECOLOGICAL INCOMPATIBILITY

Matthew (1930) has stated that "we should expect to find in a single fossil quarry that the material of each genus represents a single ecologic niche, or, if more than one, that they are quite distinct. We should not, in other words, expect to find two or more closely related species living together at the same time, within the same area, and with the same habitat, causing their remains to be preserved together in the same quarry . . . Either there would be two or more species so widely different as to belong in obviously independent ecologic niches, or else there would be one more or less variable species." This is an application to paleontological data of the general principle summed up by Cabrera (1932) as the Law of Ecologic Incompatibility in these words: "*Las formas animales afines son ecologicamente incompatibles, siendo su incompatibilidad tanto mayor, cuanto más estrecha su afinidad.*"<sup>18</sup>

The Gidley Quarry fauna is ideally adapted to the application, on one hand, and to the exemplification and corroboration, on the other, of this law and of Matthew's remarks on the taxonomy of quarry faunas. The species present in it were certainly contemporaneous, and it is highly unlikely that any of the remains can have been brought from a point so distant as to have inhabited distinctly different areas. The general environment was probably essentially the same for all, although unquestionably it included distinct ecologic niches. It is possible that deposition extended over a period of years and that there was some seasonal or other periodic change in the species of the

<sup>18</sup> I do not wish to claim for Cabrera a degree of originality that he disclaims for himself. Cabrera's law has been recognized in various forms by many authors and for a long time, but as far as I know it has never been more exactly explained and exemplified or placed more clearly on its true ecologic (not geographic) basis than by Cabrera.



neighborhood, but this is purely hypothetical. It is most reasonable to conclude that all these animals did live together, at the same time, within the same area.

It is therefore to be expected that genera present in this quarry will either have only one species each or will have species not intergrading at all and reflecting structurally their pertinence to different ecologic stations in the area. With this in mind, the assumption was made in dealing with each genus that it did include (in this quarry fauna) just one species unless the contrary could be proved beyond reasonable doubt.

Matthew, in the paper cited above, and most other writers on the question of species making in paleontology have insisted on making due allowance for variation, or using for taxonomy only nonvariable characters, but they have adduced no real, objective criterion as to what "due allowance" should be, and they sometimes seem to overlook the fact that there is no such thing as a truly and completely "nonvariable" character. Not merely as mechanical, mathematical procedures but as a general system of logic and a grouping method useful both explicitly and as an implicit background for dealing with both numerical characters and attributes, the methods of statistics provide the desired means of measuring variation accurately and the necessary criterion as to whether this variation is or is not of the sort normal within a species. These tests and this logical background have been the basis for taxonomy in this study. If the specimens pertaining to one genus could not indubitably be separated into different groups, the conclusion has been that the fundamental hypothesis of one species to each genus was correct. If they necessarily had to be separated into different groups, and these groups could not be interpreted as based on nontaxonomic differences (such as age or sex), then and only then has the hypothesis been discarded.

Since this largely objective testing has intervened, it is not arguing in a circle to start the study with the assumption that Cabrera's Law applies, and then to consider the results as a test of the validity and an example of the operation of that law. (See figs. 3 and 4.)

The actual results are as follows: Thirty genera are represented in the Gidley Quarry by one species each. Since this includes the greater part of the quarry fauna, in general it is true here that the related (congeneric) animals living at that time in this area were of the same species. The apparent exceptions belong to six genera, each of which is worthy of brief special consideration.

The multituberculates, with four species tentatively referred to *Ptilodus* and three to *Ectypodus*, are the most striking apparent exceptions. In the first place, however, the generic designations are very dubious. It is not at all certain that the species referred to

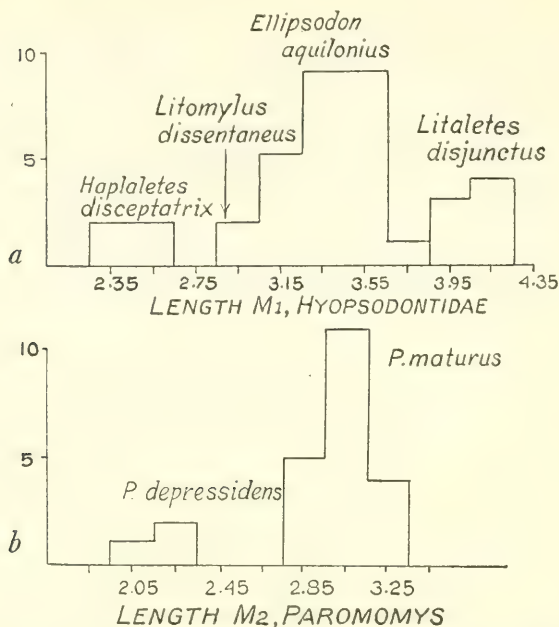


FIGURE 3.—Histograms illustrative of Cabrera's law as applied to the Gidley Quarry fauna: a, Length of  $M_1$  in hyopsodontids: in this and some other measurements the species nearly or quite intergrade, and they lived in the same place at the same time, but they are morphologically very distinct and belong to four different genera; b, length of  $M_2$  in *Paromomys*: the two species are morphologically similar, probably are congeneric, and are found together, but in this dimension and in many other characters they do not intergrade.

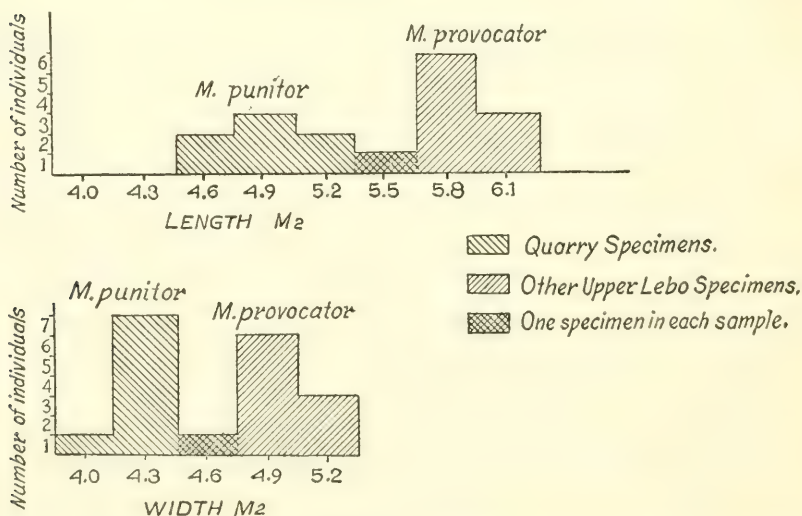


FIGURE 4.—Histogram of measurements of second lower molars of all Lebo specimens of *Metachriacus*. The distributions of these measurements, which are distributed much as are most of the characters of the samples, are clearly bimodal, and two entities are shown to be present. These entities intergrade, but they are separated by provenience, the two coming from different horizons and localities within the Lebo. They are thus interpreted as closely allied but separable species. If they occurred together, a more probable interpretation would be that they represent the two sexes of a single species.

*Ptilodus* or to *Ectypodus* are really congeneric in each case. There may well be one or more other genera represented here, although it does seem unlikely that each species could belong to a different genus. Aside from this possibility, the species referred to one genus are in every case sharply distinct from each other, with no intergradation shown. This is true of many different characters, and is well shown by table 5 of observed ranges of a few numerical characters:

TABLE 5.—Ranges of numerical characters in multituberculates, Gidley Quarry, Crazy Mountain Field, Mont.

| Genus and species        | LP <sub>4</sub> | LM <sub>1</sub> | LP <sub>4</sub> :LM <sub>1</sub> | Serrations<br>P <sub>4</sub> | Cusps M <sub>1</sub> |
|--------------------------|-----------------|-----------------|----------------------------------|------------------------------|----------------------|
| <i>Ptilodus</i> :        | <i>Mm</i>       | <i>Mm</i>       |                                  |                              |                      |
| <i>montanus</i> .....    | 7.1-9.1         | 3.2-3.7         | 2.3-2.4                          | 13-15                        | 5-6:4-5              |
| <i>douglassi</i> .....   | 6.5-6.8         | 3.7             | 1.8                              | 13                           | 6:4                  |
| <i>gidleyi</i> .....     | 5.9-6.1         | 2.5             | 2.4                              | 14-15                        |                      |
| <i>sinclairi</i> .....   | 2.5-3.7         | 1.7-2.0         | 1.3-2.0                          | 10-13                        | 6-7:4                |
| <i>Ectypodus</i> :       |                 |                 |                                  |                              |                      |
| <i>grangeri</i> .....    | 5.2-5.4         | 3.3-3.4         | 1.5-1.6                          | 13-14                        | 8:6-7                |
| <i>russelli</i> .....    | 4.9-5.1         | 2.9             | 1.7                              | 13-15                        | 10-11:6              |
| <i>silberlingi</i> ..... | 3.3             | 2.3             | 1.4                              | 12                           | 9-10:5-6             |

Thus these species probably represent more than two genera and in any case are so sharply distinct that each must have had its own ecologic niche. They do not intergrade, but in some cases, notably *P. montanus*, there are known species, in this case *P. mediaevus*, with which they do nearly or quite intergrade but which did not live together with them. In short, these are not exceptions to but are striking exemplifications of Cabrera's law.

*Leptacodon* is here credited with two species. Their tooth dimensions do not intergrade, although the degree of variation is well established for one of them, and there are structural differences such that they may well prove to be distinct subgenerically, or even generically, when both are more completely known. This is even more strikingly true of the two species referred to *Paromomys*, which are so different that I was for a time inclined to separate them generically (see fig. 3, b). *Didymictis* also is represented by two species perhaps not really congeneric, not intergrading at all and one reaching a size nearly twice that of the other.

In the case of *Claenodon*, Gidley has been followed in listing three species from the Gidley Quarry, all of about the same size and general character. Differences between them do exist, but the material is inadequate to establish the extent of variation, and when this is established I suspect that the supposed three species will prove to be variants of a single species. If not, this will be the unique example of the occurrence of two or more closely related and apparently ecologically similar species in the quarry.



## EXTENT OF KNOWLEDGE OF MIDDLE AND UPPER PALEOCENE FAUNAS

Aside from details concerning only special students, the importance of such collections as those here described lies, from a more general point of view, in the knowledge they give of the broader outlines of mammalian life in their time and area. To permit the proper drawing of inferences in this broader field, it is essential to consider the adequacy of the collections and their probable relationship to the faunas as a whole represented by them. The adequacy of a paleontological sample depends principally on three quite distinct factors:

1. The adequacy of the collection studied as a sample of the fossils actually preserved in the rocks.
2. The adequacy of the preserved fossils (collected or uncollected) as a sample of the whole fauna that actually lived in the area.
3. The adequacy of the real local fauna as a sample of the regional fauna of the whole land mass on which it lived.

Probably the best criterion of the adequacy of a collection as a sample of the preserved fossils is that of repetition. When collecting begins to pile up mainly or only duplicates, it probably has achieved sampling adequacy for the local deposit, but as long as many species remain very rare in collections, it probably has not.

Of the 51 surely separate species known from the Gidley and Silberling Quarries, 15 are here represented by only one specimen each, but of these four are known by other specimens from elsewhere in the field. Seven here have only two specimens each, but one is fairly common elsewhere. Six are here known from three specimens each, but two are also represented elsewhere. The other 23 species are represented by five or more specimens each from these quarries. In the field as a whole, of the 79 species, 19 are represented only by one specimen. Four of these represent genera still unknown elsewhere, and hence known from but one specimen each: *Stilpnodon simplicidens*, *Unuchinia asaphes*, *Elphidotarsius florencae*, and *Spanoryodon latrunculus*. Of the other 15 species here represented by only one specimen each, three (*Leptacodon* cf. *tener*, *Psittacotherium multifragum*, and *Thryptacodon ?australis*) are inseparable from species well known in other fields, and the others all belong to genera well known from other species, some of them abundant. For broader studies of morphology and faunal succession, local species are not very important, and of the 51 genera known to occur in this field, not more than five can be considered as very poorly represented in Middle Paleocene faunas generally.<sup>19</sup>

From these data, as well as the general make-up of the collections and other considerations, the collections appear to represent the real

<sup>19</sup> At least one of these, *Elphidotarsius*, and possibly one or two others are closely allied to well-known genera.

fauna <sup>20</sup> of the region fairly well but far from completely. The high proportion of species known here from only one specimen each, about 25 percent, shows that the collections, large as they are, are not yet adequate to give a proper sample of the species that may be presumed actually to be available here as fossils. Such a high percentage of very rare forms indicates clearly that any further collecting is almost certain to add to the number of known species.

As far as inference can be drawn from these data and from ecologic and similar considerations, the situation regarding the whole preserved (but only partly collected) sample, that is, the forms that were actually fossilized, is much better, but not perfectly satisfactory. It may reasonably be assumed that there was in this general region some variety among the larger and possibly plains-dwelling types, such as are common in the Torrejon and also in the later Paleocene and early Eocene in adjacent areas, but their great rarity or absence here and the general facies present strongly suggest that the conditions of deposition were such that some and perhaps many of these were not preserved and so will never be known in this area, no matter how large the collections made.

On the other hand, knowledge of the general composition of the Middle and Upper Paleocene mammalian faunas of North America as a whole may now be considered very good. It is probable that we have representatives of almost all the orders and families and a large majority of the genera,<sup>21</sup> that occurred on this continent during that time. The combined area represented by collections is now very considerable, on the order of 1,000 square miles of actual collecting territory, representing many times that in the ranges of sampled faunas. The environmental variety represented is apparently great, for the sediments yielding mammals of these ages are of many different sorts, many genera are represented by several well-defined species in each, and the inferred habits of the various known mammals include almost every possible terrestrial mammalian habitus. The collecting areas certainly were part of a unified North American land mass in the Paleocene, extend more than 1,200 miles north and south, and were probably central on that land mass, ideally situated for a representative sample of the whole North American fauna.

<sup>20</sup> It would be rather hopeless to crusade against the universal and careless habit of calling a collection a fauna. By "real fauna" is meant what should properly be called simply "fauna"; that is, the totality of mammals that actually lived in this area, and not merely those that happen to be known or the collection, a sample, on which this knowledge is based.

<sup>21</sup> In accordance with the tentative views as to adequacy of local samples expressed elsewhere (Simpson, 1936a).

## PART 2: CLASSIFICATION AND DESCRIPTION OF MAMMALS

### Order MULTITUBERCULATA Cope, 1884

Douglass' first collection included no multituberculates, but in his second collection (see Douglass, 1908) there were several teeth of this group. A jaw fragment with  $P_4$  and  $M_1$  was made type of *Ptilodus montanus*, and other specimens of that species were mentioned. Several upper teeth were referred to *Chirox*, not then known to be synonymous with *Ptilodus*, and the probable presence of other species of *Ptilodus* was mentioned. An incisor with limited enamel band (Douglass, 1908, pl. 1, figs. 18, 20) was tentatively referred to *Mixodectes* but may also be multituberculate (cf. *Eucosmodon*).

Among the first discoveries made by Mr. Silberling for the National Museum was the now famous specimen that includes skull, jaws, and some skeletal parts of *Ptilodus*. This was described, as a new species, *Ptilodus gracilis*, by Gidley (1909) in the first of his notes on this fauna. This is still the finest single multituberculate specimen known. It enabled Dr. Gidley to demonstrate that *Chirox* is merely the upper dentition of *Ptilodus* (and by analogy, *Bolodon* that of *Plagiaulax*, in the Jurassic) and for the first time to establish the true characters of this extraordinary group. He concluded that *Ptilodus* and its kin were diprotodont marsupials. Although this conclusion now seems untenable, it should be emphasized that such a conclusion was logical, if not inevitable, at the time<sup>22</sup> and that Gidley's work on this form was very able. Gidley also noted the presence of at least two other, smaller, species in the Fort Union collection, although the limited material then available did not permit their description, and he tentatively referred them to two Cretaceous species described by Marsh.

Granger and Simpson (1929), revising the Paleocene multituberculates, restudied *Ptilodus montanus*, Douglass' type, concluding that it was doubtfully distinct from *Ptilodus mediaevus* and *P. gracilis*. The latter species was not reexamined, as Dr. Gidley was then living and planning a definitive study of his material. It was suggested that no valid distinction from *P. montanus* had been given, but the species was accepted pending Dr. Gidley's definitive study. Two Torrejon specimens were doubtfully (and, as now appears, incorrectly) referred to *P. montanus*.

As regards these three species, the conclusion below is that *Ptilodus gracilis* is a synonym of *P. montanus*, which is distinct from the Torrejon *P. mediaevus*, although very closely related.

<sup>22</sup> Interesting unpublished correspondence shows, for instance, that Dr. W. D. Matthew went over Gidley's argument with great care at the time and agreed with his conclusion, although later new evidence forced him to change his mind and to reach essentially the conclusion here supported.



Dr. Gidley had evidently formed definite conclusions as to the classification of the whole group in the Fort Union collection, for most of the labels bear specific names, several of them new. Two or three of the new species described below correspond approximately with some of those recognized by Gidley, but as the correspondence is not exact even in these cases and as my classification is otherwise much unlike that suggested by Gidley's labels, it is evident that he did not employ the criteria here used. As he left no notes or manuscript relating to this group, I am forced to treat it *de novo* (except, of course, for his preliminary publication).

As shown by the figures given elsewhere, multituberculates made up a large proportion of the collection and are the most important single element in the fauna.

#### AFFINITIES OF THE MULTITUBERCULATA

This material has had such a decisive influence in the consideration of the affinities of the Multituberculata that the subject must be mentioned briefly here, although it has been thoroughly reviewed elsewhere (Simpson, 1929c, 1929e; Simpson and Elftman, 1928; Granger and Simpson, 1929).

The earliest ideas (Falconer; Owen; Marsh; Cope, 1884; Osborn, 1888), influenced by the descriptive analogy of the shearing teeth to those of some diprotodont marsupials (and a few other inconclusive characters), were that the multituberculates were marsupials. When the teeth of *Ornithorhynchus* were discovered, Cope saw in them some resemblance to the multituberculates and suggested that the latter were monotremes.<sup>23</sup>

When the fine specimen of *Ptilodus* here redescribed was discovered, it gave Dr. Gidley the first real opportunity to study the problem on a broader basis than that afforded by the often misleading dental characters. After a careful, but only provisional, analysis, he concluded that *Ptilodus* and the other multituberculates are diprotodont marsupials, diverging from those of Australia in the Jurassic or even in the earlier Triassic.<sup>24</sup>

Broom (1910) restudied *Tritylodon* and critically examined Gidley's publication, concluding that the multituberculates were an independent group without near affinities with the living monotremes, marsupials, or placentals. Later (1914) Broom studied Gidley's original and also a skull of *Taeniolabis* and then concluded that the multituberculates were monotremes.

<sup>23</sup> A few theories unworthy of further serious consideration are passed over without any notice. All have been listed and refuted in previous papers.

<sup>24</sup> This and several other points in his Fort Union work demonstrate Gidley's belief in the extreme antiquity of modern groups of mammals and their polyphyletic evolution. This philosophical consideration underlay much of his work and colored many of his conclusions. Specifically, he believed the Australian mammals to have been differentiated in the Mesozoic and outside of Australia. See also *Myrmecoboides*, below.

Matthew (first in 1915) and Granger (1915 and subsequently), however, reviewed all the evidence of Gidley and Broom and also some very important new evidence (chiefly hind limb of *Eucosmodon*) and reached a conclusion similar to Broom's first opinion, that the multituberculates are not closely related to any other known mammals. I reached this same opinion independently, and I have reviewed all the evidence and added to it in several studies.

The new evidence from the Fort Union specimens, which I had seen but not studied (except through Gidley's publication) before writing my previous papers on multituberculates, is not very extensive. I confirm Broom's opinions that the jugal is probably small in *Ptilodus* and not entering the glenoid, that there is no evidence for an alisphenoid bulla, and that there may be an uncoiled cochlea (although I consider this unproved), as well as the point already checked on other material that there is no true angular process. On the other hand Broom's evidence regarding the shoulder girdle was certainly incorrect,<sup>25</sup> and I have elsewhere indicated that the teeth do not support monotreme relationships.<sup>26</sup> The few new details regarding skull structure, foramina, etc., that I have been able to make out show a rather generalized structure with no special characters either of monotremes or marsupials. The humerus, the only known skeletal element not fully considered in my previous analysis, seems to me to be neither distinctly therian throughout, at least in a taxonomic sense, as Gidley believed,<sup>27</sup> nor in its articular portion nearer to the monotreme than to any higher type, as Broom believed. Of the two, it seems to me superficially and adaptively much nearer the Theria, but fundamentally distinct from both.

In conclusion, the present study confirms and to a slight degree strengthens my former opinion, anticipated by Matthew and Granger and still earlier by Broom but abandoned by the latter, that the multituberculates are a distinctive group not ancestral or closely related to any later mammals and of extremely ancient separation from the main mammalian stock. The very real resemblances to the Theria, pointed out by Gidley, seem to be superficial and adaptive and to indicate analogous stages of evolution, not blood relationship. The likewise real resemblances to the monotremes, pointed out by Broom, seem to be in part adaptive, in part due to the retention in two fairly conservative but not especially related lines of a few very primitive characters, inherited from the mammal-like reptiles.

<sup>25</sup> His conclusion might (but improbably) prove correct, but the evidence is not. The shoulder girdle is known only from one fragment (*Djadochtatherium*), not conclusive but rather opposed to Broom's view.

<sup>26</sup> This was the basis of Cope's belief in such relationships, and Broom added it to his table of evidence but placed no great weight on it.

<sup>27</sup> Gidley says "eutherian", which was made the subject of a correction by Broom. In fact, Gidley was right, historically, in his use of the term, since Eutheria was originally defined to include both marsupials and placentals, and he was using it in that sense. It is surely less misleading at present, however, to follow the more current usage of Metatheria for the marsupials, Eutheria for the placentals only, and Theria for both together.

## METHODS OF STUDY

The identification of this large multituberculate collection and its classification in genera and species have been peculiarly difficult, and the work was accomplished, as far as it was possible at all, only after prolonged and tedious analysis. Much of it led to no useful result and so is wholly omitted here. An outline of the useful methods employed will, however, be given, because they are similar to those used throughout this work and are in some parts unfamiliar to many paleontologists.

In the first place, it was found that although at least three, and probably four or five, genera are represented, it was not practical to begin with a generic grouping of the specimens, as is the more usual practice. The greater part of the collection consists of lower jaws. With very few exceptions, which proved to be of little practical assistance, the upper jaws all belong to a single species, and in only one case are upper and lower jaws associated. In the family Ptilodontidae the genera are usually readily distinguishable on the basis of upper teeth, but in several cases, notably *Ptilodus* and *Ectypodus*, they are practically indistinguishable from lower teeth alone. The only really clear-cut generic distinctions in the lower dentition so far recognized depend on the nature of the incisor, whether compressed and with limited enamel band or not, and in the presence or absence of  $P_3$ .<sup>23</sup> In the present collection, only a few fragmentary specimens (without cheek teeth) have an *Eucosmodon*-like incisor, and only one  $P_4$  lacks the notch for  $P_3$ . These characters are therefore not available for the bulk of the collection, and it was necessary to treat the whole collection as if it represented only one genus, to distinguish the species present, and then to attempt to place them in genera.

The following observations were made and recorded for each specimen in the collection:

## NUMERICAL:

## Dimensions:

Length of  $P_4$ .

Length and width of  $M_1$ ,  $M_2$ ,  $P^1$ ,  $P^2$ ,  $P^3$ ,  $P^4$ ,  $M^1$ , and  $M^2$ .

## Ratios:

Length  $P_4$  : Length  $M_1$ .

Length  $M_1$  : Width  $M_1$ .

Length  $M_1$  : Length  $M_2$ .

Width  $M_1$  : Width  $M_2$ .

Length  $M_2$  : Width  $M_2$ .

## Counts:

Serrations of  $P_4$ .

Cusps of  $M_1$ ,  $M_2$ ,  $P^3$ ,  $P^4$ ,  $M^1$ , and  $M^2$ .

## NONNUMERICAL:

Presence or absence of  $P_3$ .

Character of incisor.

Shape of  $P_4$ .

<sup>23</sup> The peculiarly reduced  $P_4$  of *Microcosmodon* Jepsen is also a good generic distinction, but this strange form does not occur in the present collection.



The dimensions and ratios are, from a statistical point of view, continuous variates. The counts are discontinuous variates. The nonnumerical observations are attributes and to these is to be added, for comparison with other collections, the provenience of the specimens.<sup>29</sup>

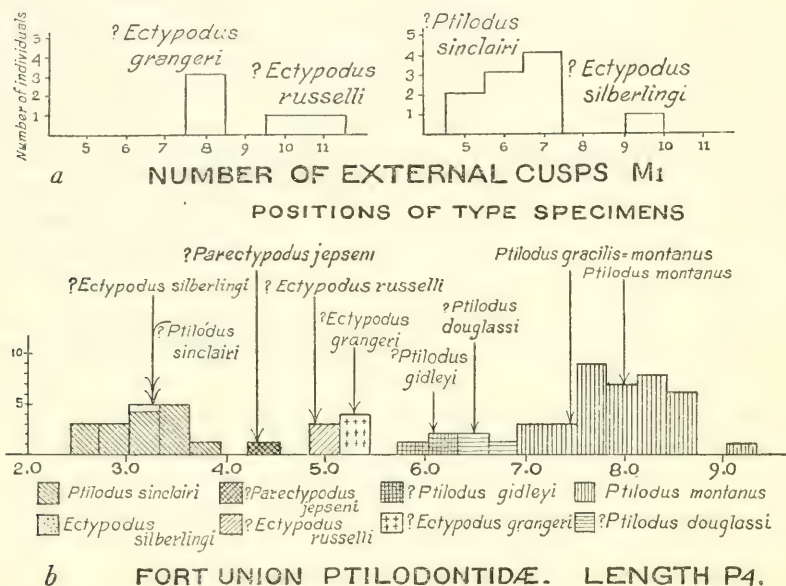


FIGURE 5.—Histograms of typical variates of multituberculates from the Gidley and Silberling Quarries: a, Number of external cusps on M1 in four species; b, length of P4 in the whole sample, with division of species based on the study of this and all other available characters.

The same data were recorded for the much fewer Torrejon specimens (American Museum collection) and, from publications, for the types of other known species available for comparison.

The numerical data were then all plotted graphically in several different ways, a few of which are here reproduced (figs. 5-7). Tentative grouping was then attempted, by taking each graphic representation and dividing it into as few groups as possible. For instance, the length of P4 histogram was at first divided into only three groups, one from 2.45 to 3.95 mm, one from 4.85 to 5.45, and one from 5.75 to 8.75. (The single specimens at 4.3 and at 9.1 were left doubtful and later disposed of as shown, on other data.)

It was then found that the groupings on different characters did not include the same specimens. For instance, in the grouping on length of P4 the type of *silberlingi* (see below) is quite indistinguishable

<sup>29</sup> Almost all are from the Silberling or Gidley Quarries, and the few that are not from these do not differ significantly. Provenience was therefore not a useful datum in sorting out the collection, but only in comparing it with other collections.

from the *sinclairi* group, but in the grouping on external cusps of  $M_1$  it is clearly distinct. Or, as another example, the *gidleyi* and *douglassi* groups are not well distinguished in either of these diagrams, but are far apart in the scatter diagram of length  $M_1$  and length  $P_4$  (as they are also in others not reproduced). By continuing this process, eight groups were eventually distinguished. A smaller number than eight was inconsistent with the distribution of two or more characters, and a larger number not necessary to interpret the distributions.

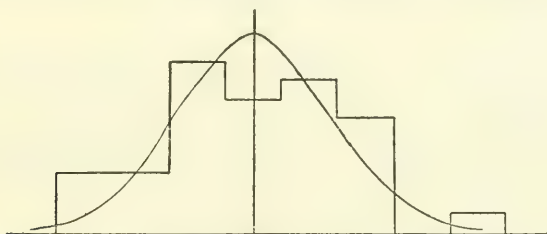


FIGURE 6.—Histogram and corresponding roughly fitted normal curve of length of  $P_4$  in *Ptilodus montanus* from the Gidley and Silberling Quarries. The distribution is the same as that for this species included in fig. 5, b.

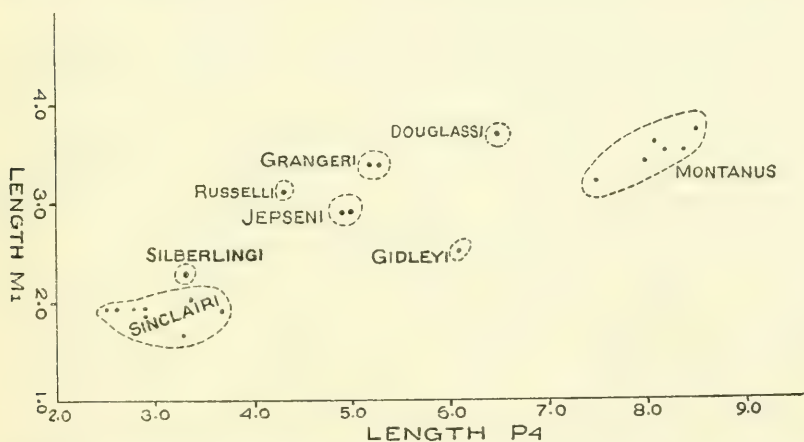


FIGURE 7.—Scatter diagram of length of  $M_1$  and length of  $P_4$  for all Gidley and Silberling Quarry specimens of multituberculates that show both of these measurements, with separation into species based on this and all other characters.

The two most abundant groups (*sinclairi* and *montanus* in the classification as finally worked out) were then tested for homogeneity, by statistical methods which showed that their deviations from normal form in any case are not of probable significance, and then for numerous continuous variates of each of these groups the mean, standard deviation, coefficient of variation, and the standard errors<sup>30</sup> of each

<sup>30</sup> I have given standard errors throughout. The probable error, which has nothing to recommend it, is 0.6745 times this figure.

of these were calculated. These new figures furnished a check on the probable taxonomic significance of the grouping. *A priori*, the range of variation allowed by the graphic grouping appeared too large for single species. Most paleontologists would think it wholly unjustified, for instance, to place a lower premolar measuring 7.0 mm in length in the same species with one measuring 9.1. But the coefficient of variation of the whole group to which these belong is only 5.3, and that is small, rather than large, for a linear dimension of teeth of a single mammalian species, so that there is no reason to believe that the graphs have permitted confusion of two species.

These statistical data, furthermore, when considered from a taxonomic biological viewpoint, suggested the degree of variation to be expected in species of this family and also gave a criterion for judging the greater or less usefulness of certain characters for taxonomic distinction. Thus, in turn, a check was possible on the groups too small for the useful calculation of these derived data.

After full consideration of all these primary and secondary data, it was clear that of the eight groups finally achieved and checked each represents a variable morphological unit, that the variation in each is not greater than commonly occurs in natural species, but that no two can be combined without producing a unit statistically heterogeneous and morphologically much more variable than a species. The biological conclusion is thus that eight species are present.

Eight species of a single family seems a relatively large number to occur at a single horizon and locality,<sup>31</sup> but there is really nothing extraordinary in this number. The ptilodontids are analogous to small rodents, and there is, for instance, hardly any region of the United States today that does not have more than eight species of Cricetidae. This large number of species clearly is not due to making the specific distinctions too small. On the contrary, since we have definite, concrete statistical data warranting this, allowance has been made for much more variation than is usually granted within a paleontological species. The largest individual of *sinclairi*, for instance, is 48 percent larger than the smallest (length of  $P_4$ ), a much greater variation than the current rule-of-thumb methods permit, although the demonstrable probability that they do belong to one species is very great.

A few specimens could not be placed in any of these eight species. A *Eucosmodon*-like lower incisor, for instance, probably does not belong with any of them. (It is also from a different locality.) Several upper teeth, not of *montanus*, cannot be associated with lower jaws, and while they almost certainly belong among the species based on

<sup>31</sup> All these species occur in the Gidley Quarry. While the specimens from the Gidley Quarry cannot all be exactly contemporaneous, they are practically so. Nevertheless the probability that they represent a succession of years or seasons helps to explain the faunal variety, not by the evolution of new species but by the opportunity for more thorough sampling of a large area.



lower teeth they must be left *incertae sedis* with respect to them. It was, however, possible to place all the lower jaws with  $P_4$ ,  $M_1$ , or both in one of these species.

It was next necessary to compare these eight species with those previously named and described. *Ptilodus mediaevus* and *trovesartianus*, the only named approximately contemporary species, demanded closest comparison. The probably later species *Ectypodus musculus*, *E. cochranensis*, *Parectypodus simpsoni*, and *P. tardus* were also compared. No others are sufficiently close to warrant detailed comparison.

At this point the attribute of provenience becomes of essential importance. As an example, the number of serrations on  $P_4$  of the *montanus* group from the Fort Union, counted on 29 individuals, varies from 13 to 15, the mean being 13.8 and the median 14. In the six available individuals of comparable size (*mediaevus* group) from the Torrejon, five have 12 and one has 13 serrations, mean 12.2, median 12. If all these be considered as one sample the distribution is:

12 serrations—5.  
13 serrations—9.

14 serrations—19.  
15 serrations—2.

The distribution shows no bimodality, and it might be assumed that the sample is homogeneous with respect to this character, but this is fallacious, as the sample is not, in fact, drawn from one population. Table 6 shows the distribution of 35 individuals with serration count of  $P_4$  and provenience considered as attributes.

TABLE 6.—Contingency table of serration counts and provenience for 35 specimens of  $P_4$  of the *Ptilodus mediaevus-montanus* group

| Serrations<br>$P_4$ | 12 | 13 | 14 | 15 |
|---------------------|----|----|----|----|
| Locality            |    |    |    |    |
| Montana-----        | 0  | 8  | 19 | 2  |
| New Mexico-----     | 5  | 1  | 0  | 0  |

Although the data are inadequate for the calculation of coefficients, it is clear that there is positive association of Montana and 14 serrations and of New Mexico and 12 serrations, and this association is of significantly greater degree than would be expected from effects of random sampling. In spite of the fact that the two samples overlap in this respect and that they could not be separated if they were from one population, it is clearly very probable that the two populations

from which they were, in fact, drawn do differ in the mean number of serrations.

Similar differences associated with provenience occur in several other characters and show that *Ptilodus mediaevus* and *P. montanus* are distinct. They could not be certainly separated if they occurred together, although even in that case the significantly greater variation of the combined samples would lead one to suspect that the population was heterogeneous.

If we accept the specific groupings finally adopted as valid, some interesting conclusions regarding variability and the value and significance of various characters for taxonomy in these animals are possible.

The length of  $P_4$ , the most useful single dimension as this is far the commonest tooth in multituberculate collections, has a coefficient of variation of  $9.3 \pm 1.6$  in the *sinclairi* group. This is high, but comparably high coefficients have been recorded for linear dimensions of teeth of mammalian species.<sup>32</sup> In the *montanus* group this coefficient is  $5.3 \pm 0.6$ . This dimension is thus much less variable in the available sample of the latter species and to that extent seems a more reliable taxonomic character for it than for the smaller *sinclairi*.<sup>33</sup> On the other hand, the length of  $M_1$  in the sample of *sinclairi* is very constant, coefficient of variation only  $4.4 \pm 1.1$ , and in *montanus* somewhat more variable, coefficient  $5.7 \pm 1.35$ .

Thus appear the interesting facts that in *sinclairi*  $P_4$  is highly variable and  $M_1$  little variable in length, while in *montanus* both are moderately, and about equally, variable. As a result of these facts, the ratio length  $P_4$  : length  $M_1$  is very much more variable in *sinclairi* (standard deviation  $0.22 \pm 0.06$ ) than in *montanus* ( $0.04 \pm 0.01$ ). This is also accentuated by the further fact that in *montanus*, but not in *sinclairi*, these two dimensions are positively correlated, that is, that in *montanus* the larger premolars tend to be associated with the larger molars, while in *sinclairi* the available data show no such tendency. Another expansion of this same unexpected and important fact, clearly visible on the scatter diagram (fig. 7), is that in *sinclairi* the line of regression of length  $M_1$  on length  $P_4$  is horizontal or even slightly inclined downward to the right, coefficient nearly zero or a very small

<sup>32</sup> E. g., in Pal. Sin., ser. C, vol. 5, fasc. 5, Helga Pearson gives coefficients up to 11.4 for  $M^3$  of one side in one sex of a single homogeneous human race and coefficients up to 8.1 for probably very homogeneous groups of fossil suids.

<sup>33</sup> How misleading the best judgment may be when not aided by statistical treatment is shown by the fact that although Gidley clearly relied on size of  $P_4$  chiefly for specific separation (as shown by the nature of his groupings and also by his unpublished specific names, all of which denote size), he placed the small *sinclairi* specimens in one species but divided the large *montanus* into three species, although the variability of the former is nearly twice that of the latter. The misleading factor is that the absolute difference in the extremes is less for the small than for the large species. Although this is the striking character to the eye, it is not the essential factor either from a statistical or from a biological point of view.

negative fraction, while in *montanus* it is inclined upward to the right, coefficient a significant, positive, fraction.<sup>34</sup> It is quite possible although unprovable from these data that the distinctly different type of variation in these two species characterizes different generic groups.

The ratio length  $M_1$  to width  $M_1$  has a standard deviation of  $0.17 \pm 0.04$  in *sinclairi* and  $0.13 \pm 0.03$  in *montanus*. The means of the two, 2.2 and 2.0, respectively, do not differ enough to prove that they are a reliable method of distinguishing these species. The character may however, be taken as of taxonomic value in such cases as that of *silberlingi* where this value, 2.6 in the unique specimen, deviates significantly from the mean for *sinclairi* (deviation more than twice the standard deviation of the latter). There is a group of species that seems to be characterized by a high value for this ratio, or descriptively by a relatively long and narrow  $M_1$ , including *silberlingi*, *russelli*, and *grangeri* in this fauna and *Ectypodus musculus* and *Parectypodus tardus* in other Paleocene American faunas.

There are too few specimens with  $M_2$  to provide adequate data, but with its variability assumed to be about that of  $M_1$ , its length:width ratio would appear to be a valuable character distinguishing *Ptilodus mediaevus* and *montanus*, in both of which the ratio averages 1.4 in the known material, from all other species in which it is known averaging 1.7 to 1.9.

The length of  $P^3$  in the *montanus* group has the very high coefficient of variation  $18.5 \pm 2.86$ . This is, generally, too high a coefficient for a sample of one species, yet the other coefficients for the upper teeth are of more reasonable size, 10.0 in the case of length  $M^1$  and considerably smaller for the other dimensions used. It is possible that some extraneous  $P^3$ 's have been included, but more probable that they are all of one species and that this tooth, in any event visibly reduced and in process of becoming vestigial, is extremely variable in length. In either case, its length is not a reliable specific character. The number of cusps on this tooth, varying from four to seven in all the specimens of this family in which it is known, seems at first sight to be a helpful character and has been used in specific diagnosis, but probably it is not. In specimens that, on all other data, rather clearly represent one species, *montanus*, this cusp number shows the full range of variation for the family, 4 to 7. The data, as well as those for *P. mediaevus*, are given in table 7.

<sup>34</sup> The samples are inadequate for the useful exact calculation of the regression equations, but their general nature is visible.



TABLE 7.—Distribution of 23 specimens of *Ptilodus montanus* and *P. mediaevus* on the basis of the number of cusps of  $P^3$ 

| Locality \ Cusps $P^3$            |                 |   |                  |   |
|-----------------------------------|-----------------|---|------------------|---|
|                                   | 4               | 5 | 6                | 7 |
| Montana ( <i>montanus</i> )----   | <sup>1</sup> 3½ | 5 | <sup>1</sup> 10½ | 1 |
| New Mexico ( <i>mediaevus</i> )-- | 2               | 1 | 0                | 0 |

<sup>1</sup> Where it is doubtful whether a cuspsule should be counted or not, I have counted the specimen as one-half for each of the groups to which it might belong.

The median for *montanus* is 6 and for *mediaevus* 4, and this may be a specific character, but the distributions fully overlap and the samples do not suffice for adequate determination of the significance of this difference. Until larger samples are at hand, this character cannot be used with certainty to distinguish species.

Passing other characters in more rapid review, the number of cusps of  $M_1$ , particularly in the outer row, shows a range of not more than 2 in each species, even in the largest samples (which are, however, small, not exceeding 9) and differ markedly from one species to another, probably affording good specific or even generic characters when the means differ by two or more. The external cusps of  $P^4$  are highly variable (range 0–3 in *montanus*) and the data inadequate for proper evaluation, but probably a marked deviation in the medians has specific significance. The inner row varies less in this material (9–10 cusps) and probably has specific value (8 in *mediaevus*), and the width of this tooth is a valuable although variable character, coefficient of variation  $8.4 \pm 1.7$  in *montanus*. The one available specimen of *mediaevus* shows a deviation from the means of *montanus* nearly three times the standard deviation of the latter, almost certainly significant. Other teeth are known in so few cases that their characters cannot be evaluated.

#### Family PTILODONTIDAE Simpson, 1927

Six valid genera of Ptilodontidae have so far been described from the American Paleocene. Their characters are summed up in the following artificial keys:

## KEY TO AMERICAN GENERA OF TERTIARY PTILODONTIDAE (LOWER JAWS)

- I. Lower incisor little or not compressed, relatively smaller, more completely enameled:
- A. Anterior base of  $P_4$  notched:
1.  $P_4$  longer than  $M_1$ , numerous serrations and strong ridges:
- a.  $M_1$  relatively longer, more cusps..... *Ectypodus*<sup>36</sup>
- b.  $M_1$  relatively shorter, fewer cusps..... *Ptilodus*<sup>36</sup>
- B. Anterior base of  $P_4$  not notched:
1.  $P_4$  longer than  $M_1$ , numerous serrations and strong ridges.. *Parectypodus*
- II. Lower incisor compressed laterally, relatively larger, enamel (below tip) more or less limited to a band:
- A. Base of  $P_4$  notched.
1.  $P_4$  longer than  $M_1$ , numerous serrations and strong ridges.. *Neoliotomus*
2.  $P_4$  shorter than  $M_1$ , few serrations and feeble ridges..... *Microcosmodon*
- B. Base of  $P_4$  not notched.
1.  $P_4$ , longer than  $M_1$ , numerous serrations and strong ridges.. *Eucosmodon*

KEY TO AMERICAN GENERA OF TERTIARY PTILODONTIDAE ( $P^4$ )

- I.  $P^4$  with two complete cusp rows and rudiments of a third..... *Ptilodus*
- II.  $P^4$  with only one complete cusp row, with rudiments of a second:
- A. Main cusp row rising posteriorly in an elevated point, noticeably anterior to the posterior end of the tooth base..... *Ectypodus*
- B. Main cusp row approximately horizontal, or arched:
1. Cusps of main row heavier, fewer, rudiment of second row stronger..... *Eucosmodon*
2. Cusps of main row smaller, more numerous, rudiment of second slight..... *Neoliotomus*
- [ $P^4$  not known..... *Parectypodus*, *Microcosmodon*

The known distribution is shown in table 8.

TABLE 8.—Known distribution of American genera of Ptilodontidae

| Genus                      | PALEOCENE                                            |                                                                                           |                                         |                | EOCENE                         |
|----------------------------|------------------------------------------------------|-------------------------------------------------------------------------------------------|-----------------------------------------|----------------|--------------------------------|
|                            | Lower (Puerco, Lower Fort Union of Clark Fork Basin) | Middle (Torrejon, Crazy Mountain Fort Union No. 2, Middle Fort Union of Clark Fork Basin) | Upper                                   |                | Lower (Sand Coulee, Gray Bull) |
|                            |                                                      |                                                                                           | A (Tiffany, Upper Fort Union, Paskapoo) | B (Clark Fork) |                                |
| <i>Ptilodus</i> .....      |                                                      |                                                                                           |                                         |                |                                |
| <i>Ectypodus</i> .....     |                                                      | ?                                                                                         |                                         |                |                                |
| <i>Parectypodus</i> .....  |                                                      | ?                                                                                         |                                         |                |                                |
| <i>Microcosmodon</i> ..... |                                                      |                                                                                           |                                         |                |                                |
| <i>Eucosmodon</i> .....    |                                                      |                                                                                           | ?                                       |                |                                |
| <i>Neoliotomus</i> .....   |                                                      |                                                                                           |                                         |                |                                |

<sup>36</sup> The distinction given may not be constant or really of generic value. The lower jaws of *Ptilodus* and *Ectypodus* show no clear generic distinction, although  $P^4$  shows them to be quite separate, although closely related genera.

Of the eight definable Fort Union species, only one, *Ptilodus montanus*, can be placed with certainty as to genus. This is well known, from the entire dentition, and is so close to the genotype of *Ptilodus* that it certainly belongs to that genus. The species *jepseni* is excluded from all named genera but *Paractypodus* and *Eucosmodon* by the absence of a notch for  $P_3$ . It does not resemble the type species of either of these genera very closely in the known parts ( $P_4$  and  $M_1$ ), but it is somewhat closer to *Paractypodus simpsoni* and may be placed, very tentatively, in the same genus. Three species, *silberlingi*, *russelli*, and *grangeri*, have what seem to be the most distinctive lower jaw characters of the type of *Ectypodus*, large length : width ratio of  $M_1$  (2.4 to 2.6 in these species, 2.5 in *E. musculus*), and large cusp number of  $M_1$  (total 14-17 in these species, 14 in *E. musculus*, typically 9-10 in *Ptilodus*). They are therefore tentatively referred to *Ectypodus*, although it is not probable that all belong to one genus or certain that any belongs to this genus. This leaves three species, *sinclairi*, *gidleyi*, and *douglassi*, which are tentatively placed in *Ptilodus*. The assignment is very uncertain in all three cases, and especially so for *sinclairi*, which, I suspect, may prove to represent a new genus when upper teeth are known, but no more probable position can be given them at present.

As previously mentioned, with this material it is now impossible to recognize genera properly, and were it not for the requirement that a species be referred to some genus it would be more satisfactory at present to consider all eight species (or the seven other than *montanus*) simply as species at large in the family Ptilodontidae.

TABLE 9.—Comparison of lower dentition of 14 species of Ptilodontidae

| Species                              | Length<br>$P_4$ | Length<br>$M_1$ | $\frac{LP_4}{LM_1}$ | $\frac{LM_1}{WM_1}$ | Serra-<br>tions<br>$P_4$ | Cusps<br>$M_1$ | $\frac{LM_1}{LM_2}$ | Remarks                                                          |
|--------------------------------------|-----------------|-----------------|---------------------|---------------------|--------------------------|----------------|---------------------|------------------------------------------------------------------|
|                                      | <i>Mm</i>       | <i>Mm</i>       |                     |                     |                          |                |                     |                                                                  |
| ? <i>Ptilodus sinclairi</i> .....    | 3.1             | 1.9             | 1.6                 | 2.2                 | 11.4                     | 6.6:4          | 1.9                 |                                                                  |
| ? <i>Ectypodus silberlingi</i> ..... | 3.3             | 2.3             | 1.4                 | 2.6                 | 12.0                     | 9.5:5.5        | 1.9                 |                                                                  |
| ? <i>Paractypodus jepseni</i> .....  | 4.3             | 3.1             | 1.4                 | 2.2                 | 11.0                     | 7:6            | -----               | No notch for $P_3$ .                                             |
| ? <i>Ectypodus russelli</i> .....    | 5.0             | 2.9             | 1.7                 | 2.5                 | 14.0                     | 10.5:6.0       | 1.8                 | Notch for $P_3$ more pronounced than in <i>E. cochranensis</i> . |
| ? <i>Ectypodus grangeri</i> .....    | 5.3             | 3.4             | 1.5                 | 2.4                 | 13.7                     | 8.0:6.7        |                     |                                                                  |
| ? <i>Ptilodus gidleyi</i> .....      | 6.0             | ca2.5           | ca2.4               | -----               | 14.3                     | 6.0:           |                     |                                                                  |
| ? <i>Ptilodus douglassi</i> .....    | 6.6             | 3.7             | 1.8                 | 2.2                 | 13.0                     | 6.0:4.0        | 1.8                 |                                                                  |
| <i>Ptilodus montanus</i> .....       | 8.0             | 3.4             | 2.3                 | 2.0                 | 13.8                     | 5.8:4.1        | 1.4                 |                                                                  |
| <i>Ptilodus mediaeetus</i> .....     | 8.3             | 3.5             | 2.3                 | 2.0                 | 12.2                     | 5.7:4.0        | 1.4                 |                                                                  |
| <i>Ptilodus trovessartianus</i> ...  | 5.9             | 3.1             | 1.9                 | 1.9                 | 13.8                     | 6:4            | 1.8                 |                                                                  |
| <i>Paractypodus simpsoni</i> .....   | 4.2             | 2.3             | 2.0                 | 2.1                 | 14                       | 8:4            | -----               | No notch for $P_3$ .                                             |
| <i>Paractypodus tardus</i> .....     | 3.0             | 1.9             | 1.6                 | 2.4                 | 10                       | 8:4            | 1.7                 | No notch for $P_3$ .                                             |
| <i>Ectypodus musculus</i> .....      | 4.0             | 2.5             | 1.6                 | 2.5                 | 13                       | 8:6            | 1.8                 |                                                                  |
| <i>Ectypodus cochranensis</i> ....   | 4.9             | -----           | -----               | -----               | 14                       |                |                     |                                                                  |



## COMPARISON OF SPECIES

A summary comparison of the lower dentitions of the eight Fort Union species and the other known species of *Ptilodus*, *Parectypodus*, and *Ectypodus* is presented in table 9. All figures are means, regardless of the size or variability of the samples, which are, in most cases, noted elsewhere. Dimensions are in millimeters. The ratios are means of individual ratios, and not ratios of the means of the dimensions involved. Fractional serrations and cusps do not exist in the raw data, but in some cases small or doubtful serrations or cusps have been counted as one-half.

The known distribution of all American Tertiary species is shown in table 10.

TABLE 10.—Known distribution of all American Tertiary species of *Ptilodontidae*

| Genera and species          | SAN JUAN BASIN |          |         | CLARK FORK-BIGHORN |                   |                  |            |                       | CRAZY MOUNTAINS  | ALBERTA  |
|-----------------------------|----------------|----------|---------|--------------------|-------------------|------------------|------------|-----------------------|------------------|----------|
|                             | Puerco         | Torrejon | Tiffany | Lower Fort Union   | Middle Fort Union | Upper Fort Union | Clark Fork | Sand Coulee-Gray Bull | Fort Union No. 2 | Paskapoo |
| <i>Ptilodus</i> :           |                |          |         |                    |                   |                  |            |                       |                  | —?       |
| <i>mediaevis</i> .....      |                | X        |         |                    |                   |                  |            |                       |                  |          |
| <i>troessartianus</i> ..... |                | X        |         |                    |                   |                  |            |                       |                  |          |
| <i>montanus</i> .....       |                |          |         |                    |                   |                  |            |                       | X                |          |
| <i>douglassi</i> .....      |                |          |         |                    |                   |                  |            |                       | X                |          |
| <i>gidleyi</i> .....        |                |          |         |                    |                   |                  |            |                       | X                |          |
| <i>sinclairi</i> .....      |                |          |         |                    |                   |                  |            |                       | X                |          |
| spp.undetermined.           |                |          |         |                    | X                 | X                |            |                       |                  | X        |
| <i>Ectypodus</i> :          |                |          |         |                    |                   |                  |            |                       |                  |          |
| <i>musculus</i> .....       |                |          | X       |                    |                   |                  |            |                       |                  |          |
| <i>grangeri</i> .....       |                |          |         |                    |                   |                  |            |                       | X                |          |
| <i>russelli</i> .....       |                |          |         |                    |                   |                  |            |                       | X                |          |
| <i>silberlingi</i> .....    |                |          |         |                    |                   |                  |            |                       | X                |          |
| <i>cochranensis</i> .....   |                |          |         |                    |                   |                  |            |                       |                  | X        |
| spp.undetermined.           |                |          |         |                    |                   | X                |            |                       |                  | X        |
| <i>Parectypodus</i> :       |                |          |         |                    |                   |                  |            |                       |                  |          |
| <i>simpsoni</i> .....       |                |          |         |                    |                   |                  |            | X                     |                  |          |
| <i>tardus</i> .....         |                |          |         |                    |                   |                  |            | X                     |                  |          |
| <i>jepseni</i> .....        |                |          |         |                    |                   |                  |            |                       | X                |          |
| spp.undetermined.           |                |          |         |                    |                   | X                | X          |                       |                  |          |
| <i>Microcosmodon</i> :      |                |          |         |                    |                   |                  |            |                       |                  |          |
| <i>conus</i> .....          |                |          |         |                    |                   | X                |            |                       |                  |          |
| <i>Eucosmodon</i> :         |                |          |         |                    |                   |                  |            |                       |                  |          |
| <i>americanus a.</i> .....  | X              |          |         |                    |                   |                  |            |                       |                  |          |
| <i>a. primus</i> .....      | X              |          |         |                    |                   |                  |            |                       |                  |          |
| <i>molestus</i> .....       |                | X        |         |                    |                   |                  |            |                       |                  |          |
| <i>teihardi</i> .....       |                | X        |         |                    |                   |                  |            |                       |                  |          |
| <i>gratus</i> .....         |                |          |         | X                  |                   |                  |            |                       |                  |          |
| <i>sparsus</i> .....        |                |          |         |                    |                   |                  |            |                       | X                |          |
| <i>Neoliotomus</i> :        |                |          |         |                    |                   |                  |            |                       |                  |          |
| <i>conventus</i> .....      |                |          |         |                    |                   |                  |            | X <sup>1</sup>        |                  |          |
| <i>ultimus</i> .....        |                |          |         |                    |                   |                  |            | X                     |                  |          |

<sup>1</sup> Jepsen now believes (personal communication) that this is older, Paleocene.

Genus *PTILODUS* Cope, 1881*PTILODUS MONTANUS* Douglass

## FIGURE 8

*Ptilodus montanus* DOUGLASS, 1908, p. 14; GIDLEY, 1909, p. 615; GRANGER and SIMPSON, 1929, p. 632.

*Ptilodus gracilis* GIDLEY, 1909, p. 616; GRANGER and SIMPSON, 1929, p. 633; *non Ptilodus gracilis* (Marsh, 1889) Osborn, 1893.

*Ptilodus admirabilis* HAY, 1930, p. 380, to replace *Ptilodus gracilis* Gidley, 1909, *non* Osborn, 1893.

*Type*.—Carnegie Museum no. 1673, left lower jaw with  $P_4$  and  $M_1$ . Collected by A. C. Silberling.

*Type of Ptilodus gracilis Gidley*.—U.S.N.M. no. 6076, skull, jaws, and partial skeleton. Collected by A. C. Silberling.

*Horizon and locality*.—Fort Union no. 2, Middle Paleocene horizons, Crazy Mountain Field, Mont..

*Diagnosis*.—Length  $P_4$ , mean  $8.0 \pm 0.07$ , standard deviation  $0.42 \pm 0.05$ . Length  $M_1$ , mean  $3.4 \pm 0.07$ , standard deviation  $0.20 \pm 0.05$ . Length  $P^4$ , mean  $5.5 \pm 0.11$ , standard deviation  $0.38 \pm 0.08$ . Width  $P^4$ , mean  $2.6 \pm 0.06$ , standard deviation  $0.22 \pm 0.04$ . Ratio length  $P_4$  : length  $M_1$ , mean  $2.3 \pm 0.02$ , standard deviation  $0.04 \pm 0.01$ . Ratio length  $M_1$  : width  $M_1$ , mean  $2.0 \pm 0.04$ , standard deviation  $0.13 \pm 0.03$ . Serrations  $P_4$  13–15, mode 14. Cusps  $P^3$  4–7, mode 6. Outer cusps  $P^4$  0–3, mode 0. Inner cusps  $P^4$  9–10, mode 9. Outer cusps  $M^1$  7–9, mode 8. Cusps  $M_1$  external 5–6, mode 6, internal 4–5, mode 4.

*Discussion*.—This is far the commonest single species in the fauna. The type happens to be almost exactly at the mean or mode for every character that it shows, and hence it is extraordinarily well fitted to be the type, although this was, of course, accidental, as it was almost unique when described. Gidley distinguished his *Ptilodus gracilis* as being slightly smaller than *P. montanus*, lower jaw far more slender, and five outer cusps on  $M_1$  as against six in *P. montanus*. The other characters given were, as Gidley recognized, not comparable with or not distinctive from *P. montanus*.  $M_1$  appears to me to have six external cusps, rather obscured by wear.<sup>37</sup> The slight size distinctions are not valid specific characters, for now that the whole collection can be compared it is seen that *P. gracilis* Gidley falls definitely within the range of *P. montanus* in every respect. It happens to be one of the smallest specimens of this species, and this unfortunate chance, not recognizable as such when he wrote his preliminary paper, misled Gidley into thinking it representative of a separate species.

<sup>37</sup> The presence of only five would not necessarily be distinctive anyway, as one specimen, surely of *montanus*, has only five and two others have five large cusps and one small and indistinct.

The circumstance that the two previously named species of Fort Union ptilodonts are synonymous makes of no interest the question whether Osborn's incorrect reference of *Cimolomys gracilis* Marsh to *Ptilodus* invalidates Gidley's later *Ptilodus gracilis* and robs Hay's name *Ptilodus admirabilis* of any *raison d'être*.

The distinction of this species from the very closely related *Ptilodus mediaevus* of the Torrejon has already been discussed in part as exemplifying the methods used in this research. The more important comparisons may be summed up as follows:

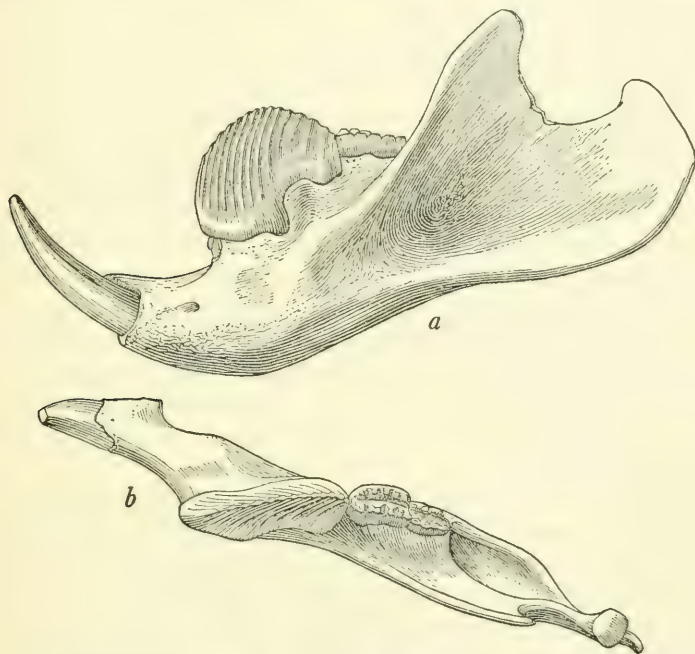


FIGURE 8.—*Ptilodus montanus* Douglass, U.S.N.M. no. 6076, left lower jaw (with some details completed from right lower jaw of same individual): a, External view; b, crown view. Three times natural size.

Most dimensions not significantly different, but in the one specimen of *P. mediaevus* that has this tooth the deviation of the width of  $P^4$  from the mean in *P. montanus* is 2.7 times the standard deviation of the latter.

Serrations of  $P_4$ , mode 14 in *P. montanus*, and of six specimens of *P. mediaevus* five have 12 and one 13.

Cusps of  $P^3$ , mode 6 in *P. montanus*, and of three specimens of *P. mediaevus* two have 4 and one 5.

External cusps of  $P^4$ , mode 0 in *P. montanus*, and one specimen of *P. mediaevus* has two. The development of this external shelf is stronger in this specimen of *mediaevus* (and in another in which the cusps cannot be surely counted) than in any specimen of *montanus*.



It is this character also that is reflected in the greater width of this tooth in *mediaevus*. Median cusps of  $P^4$  not significantly different, but internal cusps mode 9 in *montanus*, and 8 in one specimen of *mediaevus*.

The two species are certainly very closely related, but cannot be considered synonymous.

No other described species could be confused with *P. montanus*.

Thanks to the fine specimen found by Silberling and prepared and described by Gidley, *Ptilodus montanus* is the best-known multituberculate and typifies this order, the longest lived and among the most widespread of all mammalian orders, despite its extinction in the Lower Eocene. Gidley (1909) published an excellent, but explicitly provisional and preliminary, description of the best specimen, and it was later redescribed summarily, with new reconstructed sketches, by Broom (1914). It has become a classic specimen and is mentioned in practically all and figured in many of the general works on fossil mammals (e. g., Schlosser, 1923; Osborn, 1910; Romer, 1933; etc.; Scott, 1913, adds a life restoration, and Abel, 1912, a modified but incorrect reconstruction based on Gidley's figures).

The species is here briefly redescribed, as typical of family and order (or at least suborder). By taking into consideration numerous other specimens of this species, and with the help of more recently described specimens of other species, it is possible to add a few points to those previously described and also to remove the discrepancies involved in the previous descriptions.

*Dentition*.—The dental formula is  $\frac{2.0.4.2}{1.0.2.2}$ . Gidley gives  $\frac{1.1.4.2}{1.1.2.2}$ . He considered the second upper tooth as a canine, but it is surely an incisor. His inclusion of a lower canine is doubtless a *lapsus calami*, as there is no suggestion of such a tooth, and he does not mention it in his description. His premolar-molar division seems to me to be the most suitable one, although the real criterion, replacement, is not available. The ancestors of *Ptilodus* probably had five upper premolars, but it is uncertain which one was lost, and hence it is convenient to call those of *Ptilodus* simply  $P^{1-4}$ . Its lower premolars, however, are certainly  $P_{3-4}$  of the ancestral series and are so designated.

$I^1$  is a large, high-crowned, but apparently rooted tooth with a completely enameled crown. It is directed downward, forward, and inward, so that the tip must have been nearly in contact with that of its mate on the other side, although the alveoli were well spaced. The anterior face is convex and the posterior concave vertically and slightly convex transversely except for excavations at the sides. There are sharp vertical external (proximal) and internal (distal) crests, and near the tip is a more rounded posterior (lingual) crest, so that the tip is triangular in section. There are no accessory cusps.

$I^2$  is apparently present in only one specimen, the most complete one, no. 6076, and here I suspect that it is incorrectly shown. The tooth inserted in this position is an incomplete crown, with no root, bedded into the broken  $I^2$  alveolus in plaster. In size and structure it is exactly a mirror image of the same part of the  $I^1$  of the same side, right, which seems almost conclusive evidence that it is, in fact, the left  $I^1$  that was loose in the matrix and was erroneously inserted in this position. If this is true,  $I^2$  is still unknown in this species.<sup>38</sup>

$I^1$  and  $I^2$  were well spaced, and another diastema of about equal length lies between  $I^2$  and  $P^1$ . The latter tooth is tricuspid in all specimens, with three equal cusps, one anterior and a transverse pair posterior.  $P^2$  is also constant in cusp structure and resembles  $P^1$  but is wider and quadrate, with four cusps, two transverse pairs.  $P^3$  is narrower than the adjacent teeth and as shown elsewhere is extremely variable in size and in construction. There is little doubt that it is in process of reduction and that its great variability is a feature of degeneration.<sup>39</sup> The cusps are similar to those of  $P^{1-2}$  but smaller and more variable. There are always two transverse pairs, and on the bulging anterior and posterior basal parts others may be developed. When present, these are usually anterior, one or a pair, but in two specimens there is also a cusp posterior to the constant four.

$P^4$ , the upper shearing tooth, is much enlarged and has a plane, slightly inclined inner face. The internal cusp row consists of numerous small cusps (full data on cusp number are given elsewhere), united nearly to their apices and arranged in a straight anteroposterior line. External to this is another row, slightly shorter posteriorly, somewhat curved (convex externally), with fewer, larger, and more separated cusps. On the anterior part of the external face of the tooth the base bulges outward, forming a shelf which is usually vaguely papillate, without distinct cusps, but may have one or more cusps.

The premolar cusps are all similar, nearly conical, sharply pointed, the enamel furrowed and ridged radially from the point, one to three of these ridges developed into more prominent, sharp crests.

$M^1$  has three cusp rows, and these are of nearly equal length when unworn. The internal row, however, narrows anteriorly. All its cusps are relatively smaller, and anteriorly they become numerous and minute. This anterior part may be shorter than the other rows, but it is invariably sheared off very early in life by backward movements of  $P^4$ . The middle and outer cusp rows are of equal width and cusp size throughout, and the two are of about equal length. The cusp form is

<sup>38</sup> The error, if such it be, is a very natural one, especially as the tooth may have lain near the alveolus since the fragments of this specimen are very much disturbed in the matrix. Gidley notes the resemblance of the tooth to  $I^1$  except for the apparent reversal of inner and outer sides. His statement that it is smaller is true only of the apparent height, and the tooth is broken and the true height not shown.

<sup>39</sup> Reduction in the midst of the premolar series rather than at its ends may be characteristic of multituberculates. In the Plagiaulacidae of the Jurassic, it seems to be the third of the five premolars that is being reduced, and hence the *ptilodontid* premolars may be  $P^{1-2}$  and  $P^{4-5}$  of the ancestral series.

complex. The external cusps are rounded on the external face and have the more flattened internal face marked by a few deep radial furrows and intervening ridges. The internal cusps are simpler but tend to develop the same form, the furrowed side being external (toward the middle of the tooth in both cases). The cusps of the middle row are vaguely crescentic, the anterior face somewhat concave and the posterior convex, with the two sides flattened and furrowed.

$M^2$  is much shorter and very slightly wider than  $M^1$ . Internal and median rows are of about equal length, but the cusps of the middle row are larger, fewer, higher, and more separate. They are more distinctly crescentic than on  $M^1$ . The outer row is confined to the anterior half of the tooth and generally has a single crest and outer surface, so that separate cusps cannot be distinguished.

The sole lower incisor is a long, slender, curved, scimitarlike tooth with a completely enameled crown, the enamel thin on the postero-basal part and there not extending so far down. The anteroexternal face is smooth and convex, and there is a sharp anteromedial (or buccodistal) crest, next to which the internal face is excavated. There is a much weaker and shorter but similar posteroexternal (buccoproximal) crest. The long, but closed, root is inserted in a heavy collar of bone.

$I_1$  is followed by a long diastema, and homologues of  $P_{1-2}$  of the Plagiaulacidae are absent.  $P_3$  is a tiny, 1-rooted, styloform tooth, nearly circular in horizontal section, inserted vertically under the anterior edge of  $P_4$  in such a way that its crown fits tightly into a notch in the base of the latter. The crown is slightly expanded and bulbous and is enameled on the anterior face. The tooth has no function save that of buttressing  $P_4$ .

$P_4$  is the familiar large shearing tooth, which reaches its greatest known development in this genus. It has been so often described and so well figured as to require no detailed description here.  $M_1$  is a long, narrow tooth with two cusp rows. The cusps resemble those of the external and internal rows of  $M^1$  but tend to be very vaguely crescentic, concave on the posterior surfaces.  $M_2$  is wider but much shorter. The cusps are larger but less separated, in each row, and the median valley is wider and more open. The external cusp row generally extends farther posteriorly than the internal. This tooth seems to suffer more severe wear than does  $M_1$ .

*Skull.*—Seen from above, the skull is almost perfectly triangular except for the slight concavity in outline anterior to the zygoma. The orbits are almost exactly median. The skull proper is broadest, and about equally broad between the anterior and between the posterior zygomatic roots, that is, between the anterior edges of the orbits and



across the cerebellar region. The postorbital constriction is very slight and postorbital processes are lacking.

The complete, sigmoid zygoma arises nearly at the middle of the palatal region, opposite  $P^{3-4}$ .

The most striking characteristic of general outline is the extremely posterior position of the glenoid surfaces, which extend almost to the plane of the occiput, so that the basicranial region is remarkably short and wide. There are no pre- or post-glenoid and probably no paroccipital processes. The wide occipital condyle has a cochleate surface, its ventral exposure larger than the posterior.

The nasals, which are unfused, are broad, stout bones. They are slightly constricted near their middle portion, and expanded posteriorly. The nasofrontal suture, slightly curved so that the frontals are inserted into a broad and very shallow notch between the nasals, almost exactly touches at its most posterior point a line joining the most anterior margins of the two orbits. There are several small foramina in the nasals, the most prominent a pair, one near the middle of the posterior half of each nasal.

The premaxillae show no characters of interest. Their posterior facial sutures cannot be made out, or the extent of their palatal expansion, although they meet at the midline as far back as the anterior end of  $I^2$ .

The maxilla is a relatively very large bone. It has a small frontal contact above the anterior rim of the orbit.<sup>40</sup> It forms the whole anterior root of the zygoma and apparently at least half of the zygoma itself. I can detect no jugal. It may have existed as a slender bone above the zygomatic portion of the maxilla, as shown in Broom's restoration, but this is purely hypothetical. No. 9710 has the zygoma nearly complete, although fractured and dislocated, and in it no jugal is visible, so that it is quite possible that this bone was wholly lacking or fused with the maxilla. On the palate, the maxillae form a strong transverse bridge, principally between  $P^{1-2}$  of opposite sides. Anterior to this in the midline they form a pointed process between the anterior palatal foramina, which are very large and lie between but in greater part posterior to the second incisors. Posterior to the transverse palatal bridge of the maxillae is a slender median bar between the vacuities, but whether this is formed by the maxillae, palatines, or both cannot be made out. Broom (1914, p. 123) has mentioned that "the front part of the maxilla is curiously excavated as if it retained a large nasal floor cartilage." The excavation opens at the posterolateral side of the anterior palatal foramen and is cut off from the nasal passage proper by a flange of bone from the maxilla. As shown

<sup>40</sup> Broom (1914) shows maxilla and frontal separated by a small lacrimal, but this is hypothetical (dotted lines on his drawing). In fact, no lacrimal is distinguishable, and there does appear to be a definitely visible frontomaxillary contact on the right side. This region is known in several multituberculates, and none shows a lacrimal, at least outside the orbit. Probably this bone is lacking or intracranial in this order.

in another specimen (no. 9762) it runs backward into the maxilla for a short distance and ends in a blind point. An alternative, and I think slightly more probable, explanation is that this peculiar pocket lodged a nasal diverticulum. The large paired palatal vacuities, regularly long and elliptical in outline, extend from opposite the posterior end of  $P^2$  to the anterior end of  $M^1$ .<sup>41</sup>

As shown vaguely in the best skull and definitely in no. 9710, the maxillopalatine suture parallels the dental border and ends anteriorly at the rim of the vacuity opposite the anterior end of  $M^1$ . The palatines thus form the whole of the quadrangular palatal bridge principally between the first molars. In no. 9762 this is seen to be pierced on each side by a long, large, horizontal canal opening anteriorly at the vacuity and posteriorly in the basicranial region, perhaps in the choanae. The posterior palatal rim is slightly thickened.

The choanae are completely separated by a thin, vertical, median plate of bone, probably the vomer, as suggested by Broom. The palatopterygoid crests are low and rounded and do not extend downward to the level of the palate. There apparently was no hamular process.

The frontals are fairly large and cover most of the interorbital region and form the superior border of the orbits. There are thin lateral forward extensions of the parietals, which lap over the frontals, as correctly shown by Broom, but they do not reach the nasals or maxillae as in *Taeniolabis*.

The anterior branches of the sagittal crest nearly follow the parieto-frontal sutures, and the crest becomes single only near the junction with occiput and is there low. The parietals are fused on the midline, in distinction from the nasals and frontals. The presence of an interparietal, as shown in broken lines by Broom, is purely hypothetical. The parietosquamosal suture is not determinable. The large unbroken piece of bone on the left side does not show it, and this suggests that the posterior end of the suture was more lateral, and the parietal here broader, than shown in Broom's restoration.

The squamosal forms the posterior portion of the zygoma. Anterior to the glenoid surface its lower face is slightly excavated, and this may have been for the jugal, as suggested by Gidley and tentatively shown on Broom's restoration, but this is by no means certain and seems to me improbable. The glenoid surface, in any event, is wholly on the squamosal and is oval and nearly plane. From it the squamosal swings almost straight medially to the lambdoid crest.

The basicranial region is very obscure, but a few details can be made out. The anteroventral part of the occipital condyle is a very thin flange underhanging a pocket in the posterior part of which is

<sup>41</sup> They are considerably too short in Broom's restoration, the anterior margin being placed too posteriorly.

the condylar foramen, apparently single as Broom says, although a second opening may possibly have occurred along an adjacent broken area.

Farther anteromedial is another foramen, opening into a canal running forward, probably for the carotid. Between these and the temporal fossa is an elliptical opening on the skull as preserved elongate anterointernal-posteroexternally. There is some bone exposed at the posteroexternal end of this, not far from the posterointernal end of the glenoid surface. This doubtless belongs to the auditory apparatus, but I cannot identify the elements. How this opening may have been floored is not determinable, but I agree with Broom and differ from Gidley in finding no evidence that there was an alisphenoid bulla. Part of the bony internal wall of the vacuity is broken, revealing that it contains a relatively large, gently curved, cavity, interpreted by Broom as an uncoiled cochlea, a possible but not certain interpretation. The anteroexternal rim of the vacuity is formed by a ridge continuous anterointernally with the pterygopalatine crest, and posteroexternally with the squamosal stalk attaching the glenoid (and zygoma). In the lower surface of this ridge near its junction with the pterygopalatine crest is a distinct foramen. Immediately above this, more in the lateral cranial wall, is apparently another foramen, directed forward and downward. The first of these openings does not, as Gidley believed,<sup>42</sup> lead to an alisphenoid canal, and the two foramina together probably represent the foramen ovale. Above and somewhat posterior to the end of the palate, in the lateral cranial wall, is a large anterior lacerate foramen. Separate rotund or optic foramina cannot be distinguished, and they are probably confluent with this fissure. More anterior, at the same or a slightly higher level, above the anterior end of M<sup>1</sup>, is a smaller foramen, probably the ethmoid or sphenopalatine foramen.

*Mandible.*—The rodentlike form of the mandible is well shown in the figures. The symphysis is unfused.<sup>43</sup> The coronoid process is feeble, somewhat recurved, and possibly pointed—it is not quite complete in any specimen. The masseteric fossa is deep and bounded by a strong flaring flange below. The pterygoid fossa is still more pronounced and the pterygoid crest still more flaring. There is no angular process. The dental foramen is at the bottom of the deep pterygoid fossa, and the very small mental foramen is beneath the diastema.

*Vertebrae.*—There are several vertebrae, but they are so poorly preserved that little can be made out beyond the suggestion, already noted by Gidley, that neck and tail were both long and heavy.

<sup>42</sup> He said (1909, p. 619), "there appears to be an alisphenoid canal", and I assume that he was referring to this opening.

<sup>43</sup> Apparently it never fused in any multituberculate.



*Humerus*.—The head is large, oval, anteroposterior diameter slightly greater than transverse diameter. The trochanters are not preserved. The shaft is slender, deltoid crest present but weak. The entepicondyle, slightly broken, is large, and the foramen present but small. The external side of the distal end is broken, and the ectepicondylar region is not preserved. What remains of the radial articulation suggests that it was nearly spherical. The trochlea is not a broad groove bounded by a sharp crest as in later mammals (except monotremes, in which, however, these articulations are still less *Ptilodus*-like than are those of primitive Theria) but forms another subspherical, slightly crested, condyle. The fossa for the olecranon is sharp and deep.

*Ulna*.—The proximal end of the ulna has a nearly round, concave articular surface. The shaft is stout, with a strong biceps insertion. The distal end, which lacks the epiphysis, is widely expanded.

*Pelvis*.—Broom (1914) interpreted what Gidley took for the pelvis as a shoulder girdle and restored it in such a way as closely to resemble the monotreme shoulder girdle, but Granger added a note to Broom's paper (at Broom's request) pointing out that Gidley's opinion was correct. This was based on the fine *Eucosmodon* material later described by Granger and Simpson (1929) and by Simpson and Elftman (1928). There can be no doubt that the element is a pelvis, although it is so extraordinary that Broom's error was quite understandable.<sup>44</sup> The detailed descriptions of the *Eucosmodon* pelvis already published make it unnecessary to go into any detail regarding that of *Ptilodus*. As far as one can judge from the imperfect material, the two are closely similar throughout, except that in *Ptilodus* the pelvis is slenderer, with weaker muscle origins.

*Femur*.—The femur of *Ptilodus* is also much like that of *Eucosmodon*, except for being smaller and relatively weaker. The great trochanter does not rise so far above the head, and the lesser trochanter is relatively a little smaller, with less expanded head.

*Tibia and fibula*.—These bones are poorly preserved and show little except their relative sizes and the remarkably deep posteroproximal excavation of the shaft, as in *Eucosmodon*.

*Measurements* of the two types included here and the most important statistical data follow. Here, and elsewhere, I do not give all the many measurements on which these figures depend. The data are given in a form that shows all the essential and few or no nonessential figures and that makes comparison much easier and more reliable than the publication of long tables of raw data.

<sup>44</sup> In Gidley's figure (1909, fig. 4) the pelvis is restored by analogy with marsupials. The *Eucosmodon* specimen shows this restoration to be incorrect.

TABLE 11.—Measurements of *Ptilodus montanus*: Continuous variates

| Variate                                | N  | R         | M                 | $\sigma$          | V              |
|----------------------------------------|----|-----------|-------------------|-------------------|----------------|
| LP <sub>4</sub> -----                  | 36 | 7.1 -9.1  | 8.04 $\pm$ 0.07   | 0.42 $\pm$ 0.05   | 5.3 $\pm$ 0.6  |
| LM <sub>1</sub> -----                  | 9  | 3.2 -3.7  | 3.44 $\pm$ 0.07   | 0.20 $\pm$ 0.05   | 5.7 $\pm$ 1.4  |
| LP <sup>3</sup> -----                  | 21 | 2.6 -3.4  | 2.97 $\pm$ 0.12   | 0.55 $\pm$ 0.08   | 18.5 $\pm$ 2.8 |
| WP <sup>3</sup> -----                  | 21 | 2.0 -2.6  | 2.29 $\pm$ 0.03   | 0.150 $\pm$ 0.023 | 6.6 $\pm$ 1.0  |
| LP <sup>4</sup> -----                  | 12 | 4.8 -6.0  | 5.50 $\pm$ 0.11   | 0.38 $\pm$ 0.08   | 6.9 $\pm$ 1.4  |
| WP <sup>4</sup> -----                  | 12 | 2.1 -2.9  | 2.62 $\pm$ 0.06   | 0.22 $\pm$ 0.04   | 8.4 $\pm$ 1.7  |
| LM <sup>1</sup> -----                  | 9  | 4.2 -6.0  | 5.03 $\pm$ 0.17   | 0.50 $\pm$ 0.12   | 10.0 $\pm$ 2.4 |
| LP <sub>4</sub> :LM <sub>1</sub> ----- | 6  | 2.25-2.40 | 2.330 $\pm$ 0.018 | 0.045 $\pm$ 0.013 |                |
| LM <sub>1</sub> :WM <sub>1</sub> ----- | 9  | 1.8 -2.2  | 1.98 $\pm$ 0.04   | 0.13 $\pm$ 0.03   |                |

TABLE 12.—Distributions of discontinuous variates: *Ptilodus montanus*

|                                 |                                                                                                                                                                                             |                                                                                                                                                                                                                  |
|---------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Serrations P <sub>4</sub> :     | { 13-----8<br>14-----19<br>15-----2<br>5-----2<br>6-----7<br>4-----8<br>5-----1<br>4-----5<br>2-----4<br>4-----3½<br>5-----5 <sup>1</sup><br>6-----10½ <sup>1</sup><br>7-----1 <sup>1</sup> | Median cusps P <sub>4</sub> :           { 5-----1<br>6-----4<br>7-----2<br>8-----2<br>9-----7<br>10-----2<br>7-----1<br>8-----6½<br>9-----1½<br>8-----½<br>9-----5½<br>10-----2<br>3-----4<br>3-----2<br>4-----2 |
| External cusps M <sub>1</sub> : |                                                                                                                                                                                             |                                                                                                                                                                                                                  |
| Internal cusps M <sub>1</sub> : |                                                                                                                                                                                             |                                                                                                                                                                                                                  |
| External cusps M <sub>2</sub> : |                                                                                                                                                                                             |                                                                                                                                                                                                                  |
| Internal cusps M <sub>2</sub> : |                                                                                                                                                                                             |                                                                                                                                                                                                                  |
| Cusps P <sup>3</sup> :          |                                                                                                                                                                                             |                                                                                                                                                                                                                  |
| External cusps P <sup>4</sup> : |                                                                                                                                                                                             |                                                                                                                                                                                                                  |

<sup>1</sup> In all the teeth with five cusps and in all but one with six, the cusps additional to four are evidently anterior, but in one with six there is an extra anterior and an extra posterior cusp. The tooth with seven cusps has two extra anterior cusps and one extra posterior.

<sup>2</sup> That is, a slight bulging shelf, generally vaguely papillate, but without distinct cusps.

The internal cusps of M<sup>1</sup> are invariably sheared by P<sub>4</sub> at the anterior end and cannot be accurately counted in any specimen. Failure to recognize this would lead one to believe the various stages of wear typical of different species, if not genera. The outer cusps of M<sup>2</sup> are also too obscure to count in the available specimens.

This species is abundant both in the Gidley and Silberling Quarries, where its remains are among the commonest and are the best preserved of all the fossil mammals. No significant difference can be observed between the specimens from the two quarries, and the preceding data are based on the combined sample from both. Two specimens surely of this species were found at Loc. 50, and a broken P<sub>4</sub> from Loc. 51 probably belongs to it.

TABLE 13.—*Measurements of individual specimens of Pilodus montanus*

| Specimen                  | LP <sub>4</sub> | M <sub>1</sub> |     | M <sub>2</sub> |       | LP <sub>4</sub><br>LM <sub>1</sub> | LM <sub>1</sub><br>WM <sub>1</sub> | LM <sub>1</sub><br>LM <sub>2</sub> | Serra-<br>tions P <sub>4</sub> | Cusps M <sub>1</sub> | Cusps M <sub>2</sub> |
|---------------------------|-----------------|----------------|-----|----------------|-------|------------------------------------|------------------------------------|------------------------------------|--------------------------------|----------------------|----------------------|
|                           |                 | L              |     | W              |       |                                    |                                    |                                    |                                |                      |                      |
|                           |                 | L              | W   | L              | W     |                                    |                                    |                                    |                                |                      |                      |
| U.S.N.M. no. 6076-----    | Mm              | Mm             | Mm  | Mm             | Mm    |                                    |                                    |                                    |                                |                      |                      |
| Carnegie M. no. 1673----- | 7.5             | 3.2            | 1.6 | 2.2            | ----- | 2.34                               | 2.0                                | 1.4                                | 14                             | 6:4                  | 4:7                  |
| U.S.N.M. no. 6079-----    | 8.0             | 3.4            | 1.7 | -----          | ----- | 2.35                               | 2.0                                | -----                              | 14                             | 6:4                  | 4:2                  |
|                           | 8.2             | 3.5            | 1.6 | 2.6            | 2.2   | 2.34                               | 2.2                                | 1.5                                | -----                          | 6:4                  |                      |

| Specimen               | P <sub>1</sub> |     | P <sub>2</sub> |       | P <sub>3</sub> |     | P <sub>4</sub> |     | M <sub>1</sub> |     | M <sub>2</sub> |       | Cusps P <sub>3</sub> | Cusps P <sub>4</sub> | Cusps M <sub>1</sub> | Cusps M <sub>2</sub> |
|------------------------|----------------|-----|----------------|-------|----------------|-----|----------------|-----|----------------|-----|----------------|-------|----------------------|----------------------|----------------------|----------------------|
|                        | L              |     | W              |       | L              |     | W              |     | L              |     | W              |       |                      |                      |                      |                      |
|                        | L              | W   | L              | W     | L              | W   | L              | W   | L              | W   | L              | W     |                      |                      |                      |                      |
| U.S.N.M. no. 6076----- | Mm             | Mm  | Mm             | Mm    | Mm             | Mm  | Mm             | Mm  | Mm             | Mm  | Mm             | Mm    |                      |                      |                      |                      |
|                        | 2.4            | 2.1 | 2.5            | 2.5   | 2.7            | 2.1 | 4.8            | 2.5 | 4.7            | 2.1 | -----          | ----- | 6                    | 0:5½:9               | 9:9:7                |                      |
| U.S.N.M. no. 9762----- | 3.3            | 2.5 | -----          | ----- | 3.0            | 2.5 | 5.7            | 2.7 | 4.6            | 2.3 | 2.5            | 2.5   | 4                    | 0:6:9                | 8:7:7                | 71:3:3               |



**?PTILODUS DOUGLASSI** Simpson

FIGURE 9, a

*?Ptilodus douglassi* SIMPSON, 1935d, p. 225.

*Type*.—U.S.N.M. no. 9795, right lower jaw with  $P_4$ – $M_2$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry (and two referred specimens from Silberling Quarry), Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Mean length  $P_4$  (three specimens) 6.6, deviation from mean of *P. montanus* –1.4, 3.3 times standard deviation of the latter. Length  $M_1$  (type) not significantly deviating from that of *P. montanus*. Ratio length  $P_4$ :length  $M_1$  (type) 1.8, deviation from mean *P. montanus* –0.5, 12.5 times standard deviation of the latter. Length  $M_1$ :length  $M_2$  (type) 1.8, deviation from mean *P. montanus* +0.4 (standard deviation not calculable, but difference almost certainly significant). Serration and cusp number not significantly different from *P. montanus*.

*Remarks*.—Expressed in other and less definite words, the species is structurally closely similar to *P. montanus* but differs significantly in its smaller size, relatively much smaller  $P_4$ , and relatively smaller  $M_2$  (or, much larger  $M_1$  relative to  $P_4$  and  $M_2$ ).  $P_4$  also appears to be somewhat lower in lateral contour, but this cannot be adequately checked.

No species other than *P. montanus* resembles this closely enough to demand further comparison.

TABLE 14.—Measurements of individual specimens of *Ptilodus douglassi*

| U.S.N.M. no. | LP <sub>4</sub> | M <sub>1</sub> |           | M <sub>2</sub> |           | LP <sub>4</sub><br>LM <sub>1</sub> | LM <sub>1</sub><br>WM <sub>1</sub> | LM <sub>1</sub><br>LM <sub>2</sub> | Serra-<br>tions<br>P <sub>4</sub> | Cusps<br>M <sub>1</sub> | Cusps<br>M <sub>2</sub> |
|--------------|-----------------|----------------|-----------|----------------|-----------|------------------------------------|------------------------------------|------------------------------------|-----------------------------------|-------------------------|-------------------------|
|              |                 | L              | W         | L              | W         |                                    |                                    |                                    |                                   |                         |                         |
| 9795.....    | Mm<br>6.5       | Mm<br>3.7      | Mm<br>1.7 | Mm<br>2.0      | Mm<br>2.1 | 1.76                               | 2.2                                | 1.8                                | 13                                | 6:4                     | 4:2                     |
| 9888a.....   | 6.6             | -----          | -----     | -----          | -----     | -----                              | -----                              | -----                              | ?13                               | -----                   | -----                   |
| 9888b.....   | 6.8             | -----          | -----     | -----          | -----     | -----                              | -----                              | -----                              | 13                                | -----                   | -----                   |

**?PTILODUS GIDLEYI** Simpson

FIGURE 9, b

*?Ptilodus gidleyi* SIMPSON, 1935d, p. 225.

*Type*.—U.S.N.M. no. 9763, left lower jaw with  $P_4$  and broken  $M_1$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Length  $P_4$ , type, 6.1 (two other specimens 5.9 and 6.1). Length  $M_1$ , type, about 2.5. Ratio length  $P_4$ :length  $M_1$  about 2.4,

that is, not significantly different from *P. montanus* or *mediaevus* but much higher than in any other known species of this or closely related genera. Serrations  $P_4$ , type, 14 (two other specimens 14 and 15).  $P_4$  very short and high in lateral contour, rising well above the grinding plane of  $M_1$ .

*Remarks.*—Except for its somewhat more elevated  $P_4$ , this closely resembles *P. montanus* in its known proportions and other morphological features, but it is much smaller (deviation of length  $P_4$  from mean of *P. montanus* —2.0, nearly five times standard deviation of the latter), too much so to consider it a small variant of *montanus*, despite the considerable variability of the latter.

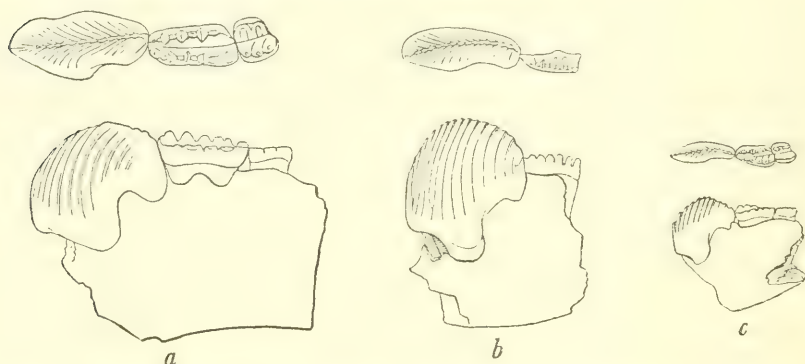


FIGURE 9.—*Ptilodus*, comparative outline drawings of lower dentition: *a*, *P. douglassi* Simpson, U.S.N.M. no. 9795; *b*, *P. gidleyi* Simpson, U.S.N.M. no. 9763; *c*, *P. sinclairi* Simpson, U.S.N.M. no. 9770. Crown and external views, all drawn as if left lower jaws (*a* and *c* reversed from right lower jaw). Three times natural size.

$P_4$  of this species is of the same size as in *P. trovessartianus*. Material is insufficient for full analysis, but if we assume the variability of both not to be much greater than in *P. montanus*, the shorter  $M_1$  of ?*P. gidleyi*<sup>45</sup> and the resulting larger ratio length  $P_4$ : length  $M_1$  are surely significant. These same differences distinguish it even more sharply from the somewhat larger species ?*P. douglassi*. No others resemble it closely.

TABLE 15.—Measurements of individual specimens of ?*Ptilodus gidleyi*

| U.S.N.M. no. | $LP_4$    | $LM_1$    | $\frac{LP_4}{LM_1}$ | Serrations<br>$P_4$ | Cusps $M_1$ |
|--------------|-----------|-----------|---------------------|---------------------|-------------|
|              | <i>Mm</i> | <i>Mm</i> |                     |                     |             |
| 9802.....    | 5.9       |           |                     | 15                  |             |
| 9763.....    | 6.1       | ca. 2.5   | ca. 2.4             | 14                  | ?6:?        |
| 9764.....    | 6.1       |           |                     | 14                  |             |

<sup>45</sup> This is not exactly determinable from the specimen, but the error of measurement can hardly exceed 0.2 mm and is almost surely less. Alveoli in a referred specimen also indicate a very short  $M_1$ .

An isolated  $P_4$  from Loc. 50 (American Museum collection) measures 6.1 mm in length, has 15 serrations, and closely resembles the type of this species in form. There can be little question that it belongs here, as it is so close to the known mean for this species and far outside the range of any other species recognized in this field.

**?PTILODUS SINCLAIRI Simpson**

FIGURE 9, c

?*Ptilodus sinclairi* SIMPSON, 1935d, p. 225.

*Type*.—U.S.N.M. no. 9770, left lower jaw with  $P_4$ - $M_2$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry (referred specimens from Silberling Quarry), Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Length  $P_4$ , mean  $3.1 \pm 0.07$ , standard deviation  $0.29 \pm 0.05$ . Length  $M_1$ , mean  $1.9 \pm 0.03$  standard deviation 0.08. Ratio length  $P_4$ : length  $M_1$ , mean  $1.6 \pm 0.08$  standard deviation  $0.22 \pm 0.06$ . Ratio length  $M_1$ : width  $M_1$ , mean  $2.2 \pm 0.06$ , standard deviation  $0.17 \pm 0.04$ . Serrations  $P_4$  10-13, mode 12. Cusps  $M_1$  6-7:4, mode 7:4.

*Remarks*.—Some of the peculiarities of this species, second only to *P. montanus* in abundance, have already been discussed above. Its very small size at once distinguishes it from any species of related genera except ?*Ectypodus silberlingi* (diagnosed below), and *Parectypodus tardus*, with which it cannot be congeneric, as it has  $P_3$ .

The two specimens (6089 and 6090, and also a third, 6149, so labeled but not published by number) that Gidley at first (1909, p. 623) referred to "*Ptilodus formosus*?" (Marsh) (= *Halodon formosus* Marsh) belong to ?*Ptilodus sinclairi*.<sup>46</sup> Adequate comparison with the fragmentary Cretaceous types of Marsh is impossible, but in view of the very different age and of the fact that when close comparison is possible not only the species but also the genera are very distinct, it may, I think, be assumed that the Fort Union forms do not belong to Cretaceous species.

As noted above, it is improbable that this species belongs to *Ptilodus*, but it cannot at present be clearly distinguished from that genus.

<sup>46</sup> Gidley did not change their labels, but it is practically certain that he recognized their pertinence to a distinctive species. He recognized ?*Ptilodus sinclairi* (under a different, unpublished name), and so labeled about half the specimens that I place here, covering almost the same range of variation, so that in this case his specific criteria and mine lead to nearly the same result. He also included, however, one or two specimens that I place in other species.



The principal numerical data on this form are as follows:

TABLE 16.—*Measurements of ?Ptilodus sinclairi: Continuous variates*

| Variate                                | N  | R         | M         | $\sigma$    | V       |
|----------------------------------------|----|-----------|-----------|-------------|---------|
| LP <sub>4</sub> -----                  | 16 | 2.5-3.7   | 3.13±0.07 | 0.29 ±0.05  | 9.3±1.6 |
| LM <sub>1</sub> -----                  | 8  | 1.7-2.0   | 1.88±0.03 | 0.083±0.021 | 4.4±1.1 |
| LP <sub>4</sub> :LM <sub>1</sub> ----- | 8  | 1.32-1.95 | 1.61±0.08 | 0.22 ±0.06  |         |
| LM <sub>1</sub> :WM <sub>1</sub> ----- | 8  | 1.9-2.4   | 2.25±0.06 | 0.17 ±0.04  |         |

TABLE 17.—*Distributions of discontinuous variates: ?Ptilodus sinclairi*

|                                      |   |         |                                      |        |
|--------------------------------------|---|---------|--------------------------------------|--------|
| Serrations P <sub>4</sub> :-----     | { | 10----3 | Internal cusps M <sub>1</sub> :----- | 4----7 |
|                                      |   | 11----5 | External cusps M <sub>2</sub> :----- | 4----3 |
|                                      |   | 12----7 | Internal cusps M <sub>2</sub> :----- | 2----3 |
| External cusps M <sub>1</sub> :----- | { | 6----3  |                                      |        |
|                                      |   | 7----4  |                                      |        |

TABLE 18.—*Measurements of individual specimens of ?Ptilodus sinclairi*

| U.S.N.M.<br>no. | LP <sub>4</sub> | M <sub>1</sub> |     | M <sub>2</sub> |     | LP <sub>4</sub><br>LM <sub>1</sub> | LM <sub>1</sub><br>WM <sub>1</sub> | LM <sub>1</sub><br>LM <sub>2</sub> | Serra-<br>tions<br>P <sub>4</sub> | Cusps<br>M <sub>1</sub> | Cusps<br>M <sub>2</sub> |
|-----------------|-----------------|----------------|-----|----------------|-----|------------------------------------|------------------------------------|------------------------------------|-----------------------------------|-------------------------|-------------------------|
|                 |                 | L              | W   | L              | W   |                                    |                                    |                                    |                                   |                         |                         |
| 9797-----       | Mm              | Mm             | Mm  | Mm             | Mm  | 1.37                               | 2.4                                | 2.1                                | 10                                | 7:4                     | 4:2                     |
| 9792-----       | 2.6             | 1.9            | 0.8 | 0.9            | 0.9 | 1.53                               | 2.4                                | 1.7                                | 12                                | ?                       | ?                       |
| 9770-----       | 2.9             | 1.9            | 0.8 | 1.1            | 0.9 | 1.94                               | 1.9                                | 1.9                                | 11                                | 6:4                     | 4:2                     |
| 9791-----       | 3.3             | 1.7            | 0.9 | 0.9            | 0.8 | 1.95                               | 2.4                                | 2.1                                | 12                                | 6:4                     | 4:2                     |
|                 | 3.7             | 1.9            | 0.8 | 0.9            | 0.9 |                                    |                                    |                                    |                                   |                         |                         |

These four best specimens include practically all the extremes in these characters.

A P<sub>4</sub> collected by A. C. Silberling on January 21, 1903, now in the Princeton University collection, measures 3.0 mm in length and has 12 clear serrations and 1 obscure. It is indistinguishable in any way from some of the smaller variants of *Ptilodus sinclairi* from the Gidley Quarry and is referred to that species. Nothing like it has been discovered at a Lower Paleocene horizon, nor is it exactly matched in any of the many Lance specimens (*Cimolomys, sensu lato*) known to me. It bears the horizon designation "Puerco" (by which was then meant approximately the series later called Fort Union No. 1), the number 14, and the locality "Moen and Beck" (a very general locality including a large area along Bear Butte). Mr. Silberling informs me positively that this is from Loc. 65, and this can be taken as correct. The specimen is thus the oldest mammal ever found in this field.

Genus *ECTYPODUS* Matthew and Granger, 1921*?ECTYPODUS GRANGERI* SimpsonFIGURE 10, *a**?Ectypodus grangeri* SIMPSON, 1935d, p. 226.

*Type*.—U.S.N.M. no. 9801, left lower jaw with  $P_4$ – $M_1$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Length  $P_4$ , type and mean of four specimens, 5.3. Length  $M_1$ , type and mean of three specimens, 3.4. Ratio length  $P_4$ : length  $M_1$ , type 1.56, referred specimen 1.53. Length  $M_1$ :width  $M_1$ , type 2.6, mean of three specimens, 2.4. Serrations  $P_4$ , type 14, other specimens, two 14, one 13. Cusps  $M_1$ , type, 8:7, other specimens one 8:7, one 8:6. Apex of  $P_4$  nearly on a level with grinding surface of  $M_1$ .

*Remarks*.—Like the other two new species tentatively referred to *?Ectypodus*, below, this differs from all species referred to *Ptilodus* in the large length:width ratio and large cusp number of  $M_1$ , characters that appear to be surely significant and make closer comparison with species of *Ptilodus* unnecessary. This, and the next two species, are excluded from *Parectypodus* by the presence of  $P_3$ .

The present form compares very closely with *Ectypodus musculus* in all its visible characters. In spite of the small size of the samples, the considerably greater size of *?E. grangeri* is almost certainly significant, and its association with wide geographic separation and with a distinct difference in age shows the species to be distinct.

The principal measurements are given in table 19.

TABLE 19.—Measurements of individual specimens of *?Ectypodus grangeri*

| U.S.N.M.<br>no. | LP <sub>4</sub> | M <sub>1</sub> |           | LP <sub>4</sub><br>LM <sub>1</sub> | LM <sub>1</sub><br>WM <sub>1</sub> | Serra-<br>tions<br>P <sub>4</sub> | Cusps<br>M <sub>1</sub> |
|-----------------|-----------------|----------------|-----------|------------------------------------|------------------------------------|-----------------------------------|-------------------------|
|                 |                 | L              | W         |                                    |                                    |                                   |                         |
|                 | <i>Mm</i>       | <i>Mm</i>      | <i>Mm</i> |                                    |                                    |                                   |                         |
| 9800.....       | 5.2             | 3.4            | 1.6       | 1.53                               | 2.1                                | 14                                | 8:6                     |
| 9801.....       | 5.3             | 3.4            | 1.3       | 1.56                               | 2.6                                | 14                                | 8:7                     |
| 9773.....       | 5.4             |                |           |                                    |                                    | 13                                |                         |
| 9782.....       | 5.4             |                |           |                                    |                                    | 14                                |                         |
| 9771.....       |                 | 3.3            | 1.3       |                                    | 2.5                                |                                   | 8:7                     |

*?ECTYPODUS RUSSELLI* SimpsonFIGURE 10, *b**?Ectypodus russelli* SIMPSON 1935d, p. 226.

*Type*.—U.S.N.M. no. 9765, left lower jaw with  $P_4$ – $M_2$ . Collected by A. C. Silberling.

*Horizon and locality.*—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—Length  $P_4$ , type and mean of three, 5.0. Length  $M_1$ , type and referred specimen, 2.9. Ratio length  $P_4$ :length  $M_1$ , type and referred specimen, 1.7. Length  $M_1$ :width  $M_1$ , type 2.4, referred specimen 2.6. Serrations  $P_4$ , type 14, others one 15, one 13. Cusps  $M_1$ , type 10:6, referred 11:6. Cusps  $M_2$ , type and referred specimen 5:2. Crest of  $P_4$  elevated well above  $M_1$ .

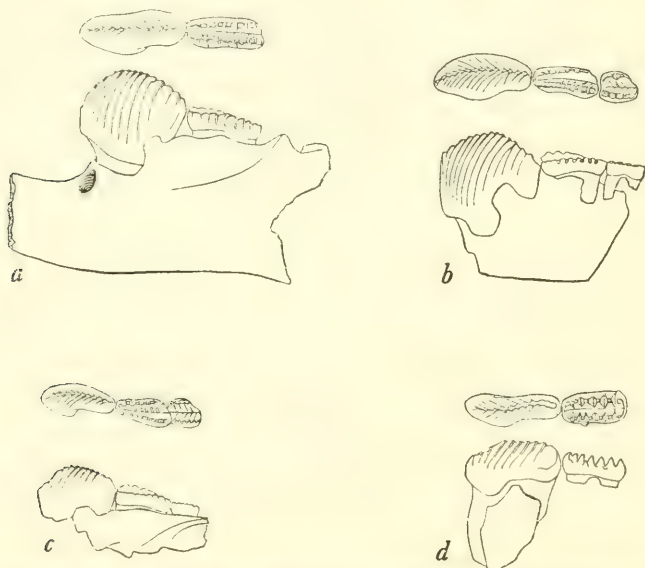


FIGURE 10.—*Ectypodus* and *Parectypodus*, comparative outline drawings of lower dentitions: a, *E. grangeri* Simpson, U.S.N.M. no. 9801; b, *E. russelli* Simpson, U.S.N.M. no. 9765; c, *E. silbertingi* Simpson, U.S.N.M. no. 9798; d, *P. jepseni* Simpson, U.S.N.M. no. 9769. Crown and external views, left lower jaws. Three times natural size.

*Remarks.*—This species considerably resembles the preceding one, and I was at first inclined to consider its smaller size as due only to variation, as it is well within the possible size limits. That would, however, make the range in  $M_1$  external cusp number for the combined species twice as great as has been demonstrated for any known species of this or allied genera, even in much larger samples, and the probability is very greatly against this occurring in a single species and against the association of larger cusp number with smaller size being due to accidents of sampling. It is possible also, although less clear, that association with a slightly larger length  $P_4$ :length  $M_1$  ratio is significant. The added character of a more elevated  $P_4$  makes the specific distinction practically certain.

$P_4$  of this species very closely resembles that of *Ectypodus cochranensis*. However: (a) It here has a definitely larger notch for  $P_3$ , (b) the localities are well separated, (c) the ages are distinctly



different, (d) only  $P_4$  can be compared, and (e) extremely slight differences in this tooth are commonly associated with specific or even generic differences in other parts of the dentition.<sup>47</sup>

In size this species is a little closer to *E. musculus* than is *E. grangeri*, although still definitely larger, but its other distinctions from *E. grangeri* are distinctive in about the same degree from *E. musculus*.

A tooth of this species (no. 6088) was referred by Gidley to "*Ptilodus serratus*" (= *Halodon serratus* Marsh) in his preliminary publication (1909, p. 622) but with the reservation that it might later be placed in a new species. Had he completed his work, Dr. Gidley would unquestionably have placed this specimen in a new species, as is done here. The remarks made above, regarding specimens of *?Ptilodus sinclairi* referred tentatively to "*Ptilodus formosus*" are equally apropos here.

TABLE 20.—Measurements of individual specimens of *?Ectypodus russelli*

| U.S.N.M. no. | LP <sub>4</sub> | M <sub>1</sub> |        | M <sub>2</sub> |        | LP <sub>4</sub><br>LM <sub>1</sub> | LM <sub>1</sub><br>WM <sub>1</sub> | LM <sub>1</sub><br>LM <sub>2</sub> | Serrations<br>P <sub>4</sub> | Cusps<br>M <sub>1</sub> | Cusps<br>M <sub>2</sub> |
|--------------|-----------------|----------------|--------|----------------|--------|------------------------------------|------------------------------------|------------------------------------|------------------------------|-------------------------|-------------------------|
|              |                 | L              | W      | L              | W      |                                    |                                    |                                    |                              |                         |                         |
| 9766-----    | Mm 4.9          | Mm 2.9         | Mm 1.1 | Mm 1.6         | Mm 1.5 | 1.69                               | 2.6                                | 1.8                                | 13                           | 11:6                    | 5:2                     |
| 9765-----    | 5.0             | 2.9            | 1.2    | 1.5            | 1.4    | 1.72                               | 2.4                                | 1.9                                | 14                           | 10:6                    | 5:2                     |
| 6088-----    | 5.1             |                |        |                |        |                                    |                                    |                                    | 15                           |                         |                         |

**?ECTYPODUS SILBERLINGI Simpson**

FIGURE 10, c

*?Ectypodus silberlingi* SIMPSON, 1935d, p. 226.

*Type*.—U.S.N.M. no. 9798, left lower jaw with incisor and  $P_4$ - $M_2$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—(Only one specimen.) Length  $P_4$ , 3.3. Length  $M_1$ , 2.3. Ratio length  $P_4$ :length  $M_1$ , 1.4. Length  $M_1$ :width  $M_1$ , 2.6. Serrations  $P_4$ , 12. Cusps  $M_1$ , 9-10:5-6.<sup>48</sup> Crest of  $P_4$  relatively low.

*Remarks*.—In most of its characters, this species falls well within the range of *?Ptilodus sinclairi*, with which it would be confused in casual examination, but its deviation from the mean of *sinclairi* in length of  $M_1$  is 5 times the standard deviation of the latter, and in the ratio length  $M_1$ :width  $M_1$ , 2.3 times, and the marked difference in cusp number of  $M_1$  is also surely significant. The species cannot be, and the genera probably are not, the same.

<sup>47</sup> Russell (1929, p. 173) in describing *E. cochranensis* was doubtless referring to my *?E. russelli* when he wrote, "Undescribed premolars of about the same size as *E. cochranensis* occur in the Fort Union beds of Montana, but these teeth differ markedly from the present specimen in having a pronounced undercutting in the anterior margin of the crown."

<sup>48</sup> That is, clearly at least 9:5, and in each row rudiments of another cusp so that it is doubtful whether the count should be 9:5 or 10:6.

Among other species, it most closely resembles *Ectypodus musculus*, but aside from the different horizon and locality it differs in being somewhat, perhaps significantly, smaller and in having more cusps on  $M_1$ , as well as other minor distinctions that may prove also to be significant when a larger sample permits their evaluation.

Measurements of the type other than those given above: Width  $M_1$ , 0.9; length  $M_2$ , 1.2; width  $M_2$ , 1.0; ratio length  $M_1$ :length  $M_2$ , 1.9; cusps  $M_2$ , 25:3.

**?ECTYPODUS species**

U.S.N.M. no. 9772 includes three unassociated last upper premolars, one broken, from the Gidley Quarry. They have one complete row of 11 cuspules, or serrations, and a rudimentary anteroexternal basal row of 2 cusps, both strong and distinct, the more posterior larger and opposite the third or fourth cusp of the main row. These teeth suggest *Ectypodus musculus*, but the elevation of the posterior end of the main crest is less than in that species, and the apex is not on the most posterior cuspule but on the fourth or fifth from the posterior end. *Neoliotomus conrentus* is inadequately known, but apparently these specimens are less symmetrical in lateral contour. Size and cusp number surely distinguish the species from any comparable form, and the generic reference is doubtful. The lengths of the two more complete teeth are 4.8 and 4.5 mm.

These probably represent the upper dentition of one of the species here named from lower jaws, and by inference somewhat more probably one referred to *?Ectypodus*, but the association cannot be established. From the ratio length  $P_4$ :length  $P^4$  in *Ectypodus musculus* (1.48), the lower  $P_4$  should be 6.7–7.1 mm in length, about as in *?Ptilodus douglassi*, but the latter has no characters suggesting *Ectypodus*. *?Ectypodus grangeri* may be based on the corresponding lower teeth, but it seems somewhat too small.

**Genus PARECTYPODUS Jepsen, 1930**

**?PARECTYPODUS JEPSENI Simpson**

FIGURE 10, d

*?Parectypodus jepseni* SIMPSON, 1935d, p. 227.

*Type*.—U.S.N.M. no. 9769, left lower jaw with  $P_4$ – $M_1$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union No. 2, Crazy Mountain Field, Mont.

*Diagnosis*.—(Only one specimen.) Length  $P_4$ , 4.3. Length  $M_1$ , 3.1. Ratio length  $P_4$ :length  $M_1$  1.4. Length  $M_1$ :width  $M_1$ , 2.2. Serrations  $P_4$ , 11. Cusps  $M_1$ , 7:6.  $P_4$  long and low. No notch for  $P_3$ .

*Remarks*.—This can be compared only with the later *Parectypodus simpsoni*. Its longer  $M_1$ , lower length  $P_4$ :length  $M_1$  ratio, smaller

serration number, markedly different cusp formula of  $M_1$ , and other lesser differences show it to be markedly distinct. It differs even more, but in somewhat different ways, from *Parctypodus tardus*. The generic reference is very dubious.

Measurements of the type other than those given above: Width  $M_1$ , 1.4.

Genus *EUCOSMODON* Matthew and Granger, 1921

*EUCOSMODON SPARSUS*,<sup>49</sup> new species

FIGURE 11

*Type*.—U.S.N.M. no. 10113, part of lower incisor, with a small adherent jaw fragment. Collected by A. C. Silberling.

*Horizon and locality*.—Loc. 25, and referred specimens from Loc. 51 and the Silberling Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Type incisor, maximum transverse diameter 4.0, minimum 1.4 mm, ratio 2.86.

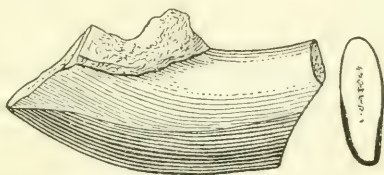


FIGURE 11.—*Eucosmodon sparsus*, new species, U.S.N.M. no. 10113: Part of lower incisor and fragment of jaw. External view and cross section at anterior end of incisor as preserved, with enamel band shown in heavier outline. Four times natural size.

*Remarks*.—This is an interesting form worthy of formal record despite the imperfection of the material. Poor as this is, it fulfills the practical requirements of demonstrating distinction from any comparable species and ensuring that better specimens, when found, can be securely determined as of this species.<sup>50</sup> The occurrence of three essentially similar specimens from three different localities and horizons, but all within this field and all in the No. 2 beds, covering a short span of time, also seems to demonstrate the validity and considerable range of the species.

U.S.N.M. no. 9861 is a broken incisor from the Silberling Quarry and no. 9705 a similar specimen from Loc. 51. Their dimensions, given below, agree closely with those of the type.

In maximum diameter these teeth approach *E. americanus primus* and are significantly smaller than other comparable species. In minimum diameter they are somewhat less and in compression ratio

<sup>49</sup> *Sparsus*, scattered, from the dispersion of the scanty known remains of the species.

<sup>50</sup> Such specimens are almost surely included in the American Museum collection, but they are not yet prepared, and in any event it is proper that types be from the older collection, as far as possible.



significantly more than *E. a. primus*. The minimum diameter is about that of *E. teilhardi*, but the maximum diameter and the compression are significantly less. *E. americanus* and *E. molestus* have the incisors significantly larger in both diameters and the compression less. Exact comparison with *E. gratus* Jepsen is not possible, but the incisor alveolus of that species measures 2.7 by 1.1 mm, ratio 2.45. The alveolus, and of course therefore the incisor as well, are much smaller than the incisor of *E. sparsus*. No known species aside from the several now mentioned could well be so closely related to *E. sparsus* as to demand differentiation.

TABLE 21.—Comparison of data on lower incisors of Eucosmodon

| Species and specimen                           | Diameters |           | Ratio  |
|------------------------------------------------|-----------|-----------|--------|
|                                                | Maximum   | Minimum   |        |
|                                                | <i>Mm</i> | <i>Mm</i> |        |
| <i>E. americanus</i> , type.....               | 6.0       | 2.7       | 2.22   |
| <i>E. a. primus</i> , paratype.....            | 4.2       | 1.9       | 2.21   |
| <i>E. molestus</i> , neotype.....              | 5.8       | 2.6       | 2.23   |
| <i>E. teilhardi</i> , paratype.....            | 5.2       | 1.6       | 3.25   |
| <i>E. sparsus</i> { Means.....                 | 4.3       | 1.5       | 2.70   |
| { 10113.....                                   | 4.0       | 1.4       | 2.86   |
| { 9705.....                                    | 4.1       | 1.6       | 2.56   |
| { 9861.....                                    | 4.0       | 1.5       | 2.67   |
| ( <i>E. gratus</i> , type, from alveolus)..... | (2.7)     | (1.1)     | (2.45) |

The original of Douglass' plate 1, figures 18 and 20, probably belongs to this genus. If the scale of the figure is accurate (which is not invariably true in cases where I have studied Douglass' originals), the maximum diameter is about 3.7 mm, smaller than other specimens referred to this species, to which the specimen may nevertheless belong.

### Order INSECTIVORA Gray, 1827

Forms that are at least nominally referable to the Insectivora constitute an important element in Paleocene and Eocene faunas, and this is particularly true in faunas, like that here described, in which the microfauna is well or disproportionately represented. They are abundant in the present collection, including at least 10 species, all of which occur together in the Gidley Quarry.

Despite diverse specializations, such as in the incisors of the Soricoida or the limbs of the Talpoidea, the recent insectivores are on the whole the most primitive of living placental mammals. The characters common to all of them, excluding the specializations of various particular phyla or larger groups, are in general those unquestionably primitive for all placental mammals. The conception of the order and its definition thus do not so much depend on special

characters developed within the order as on characters also basic for other orders but generally lost or more profoundly modified in those orders. Indeed the outstanding ordinal character of the Insectivora, paradoxically, is the absence of ordinal characters, in the sense that these are developed in other groups.

Although the order is thus necessarily more loosely knit than is usual, it does not follow that it is altogether artificial. The retention of so many primitive characters is in itself some indication that this conservative group may have still been somewhat unified after the more progressive orders had acquired their distinctive characters. Furthermore, there are a few characters, such as those noted by Matthew in the astragalus, not of wholly generalized placental pattern and distinctive of the Insectivora as against many or most other mammals. There are also some characters, like the peculiar specializations of the incisors, that do not occur in all insectivores and are occasionally paralleled in other orders but that nevertheless appear so frequently among insectivores that they seem to reflect a certain genetic tendency and to help to bind the group together.

Every individual living insectivore is a specialized animal, each species in its own way, and none can be considered, even structurally, as really representing the general placental ancestry in any very exact sense of the words. Yet the abstract conception Insectivora based on all known forms is such that it would, almost perforce, include the most primitive placental mammals. Probably the most remote ancestors (in the Cretaceous) of most, perhaps of all, the placental orders would be referable to the Insectivora by definition. In this sense the order Insectivora is prototypal and ancestral to all others among the Placentalia.

Because the ordinal characters of the Insectivora are mainly primitive and because most of the Paleocene mammals are primitive, almost all known Paleocene forms resemble the Insectivora in many respects. If we knew the archaic mammals of the Paleocene but had no knowledge of any of the forms that lived between that time and the Recent, it would be a much more logical and practical system to refer almost all Paleocene mammals to the Insectivora,<sup>51</sup> rather than to distribute them in numerous different orders as is now the usual practice. This distribution, in accordance with a "vertical" or so-called evolutionary conception of classification, is accomplished by the recognition of fossils intermediate between the Paleocene groups and the more distinctly separated later orders and of incipient specializations within the Paleocene groups themselves that point toward groups later to become so distinct that they are granted ordinal rank.

<sup>51</sup> This is approximately the sense of Cope's *Bunotheria*, a broad group including the Insectivora and various other primitive mammals. Cope did, however, separate and distribute among other orders some Paleocene mammals, such as the *Condylarthra*, that were on the whole as primitive as those included in the *Bunotheria*.

The concept Insectivora as it is applied to the Paleocene (and Eocene) faunas may thus include four different sorts of lesser groups:

1. Very primitive placentals whose ancestral relationship to other later groups is not now recognizable. Naturally we do not know what groups may be included here, for the only way in which this situation could be shown to exist would be by recognition of the relationships, but probably some so-called insectivores are of this character.

2. Animals that are in fact in or near the ancestry of later more specialized insectivores and that are therefore Insectivora *sensu stricto*. The Nyctitheriidae probably belong in this category, although the relationship is not definitely established. The other families in the present fauna almost surely are not Insectivora in this special and most limited sense.

3. Animals not structurally representative of the ancestry of later insectivores but sharing certain specializations with them that seem to indicate that they arose from a common stock with the later groups after the definite differentiation of that stock. These are also to be considered as Insectivora in a strict sense, even though the usage is broader than it is as applied to the second category. The degrees of such collateral relationship vary greatly. Thus the Leptictidae fall definitely in this category, as they share many and apparently significant special characters with the Erinaceidae, although clearly not ancestral to that family. The Pantolestidae likewise show evidence of a special collateral relationship to the later insectivores, but the resemblance is less particular and the relationship evidently more remote.

4. Groups that were derived from the nominally insectivore protoplacental stock but that had begun to diverge markedly from any other groups, without, however, having a sufficiently long history, being sufficiently important faunal elements, or acquiring sufficiently striking special characters to warrant the erection for them of a special order. Such groups are clearly Insectivora only in a very broad sense, yet their exclusion from the order would be a needless complication of taxonomy. The Mixodectidae appear to belong to this category.

In this fauna there are 10 genera that are referable to the Insectivora in the general sense here accepted. *Gelastops* is evidently related to *Didelphodus* of the Lower Eocene and *Acmeodon* of the Middle Paleocene. It is perhaps a modified survivor of the protoplacental stock. *Prodiacodon* and *Leptacodon* are typical leptictids, *Myrmecoboides* is an aberrant member of that group, and *Bessoecetor* is a primitive but typical pantolestid, while *Aphronorus* constitutes with the Torrejon *Pentacodon* a more aberrant group probably of pantolestid origin. *Eudaemonema* seems surely to be a mixodectid, although



phyletically distinct from any other known genus. *Picrodus* is really of unknown affinities and is placed in the Insectivora only in default of other evidence.

Family ?DELTATHERIDIIDAE Gregory and Simpson, 1926

Subfamily DIDELPHODONTINAE Matthew, 1918

Matthew placed this subfamily in the Leptictidae, pointing out that the affinities of *Didelphodus* are uncertain, but that it "can not easily be placed in any other family." Except for the general statement that "the teeth are in many respects not unlike those of the Leptictidae", he gave no definite reason for placing *Didelphodus* in that family, where it was decidedly anomalous. In defining the Deltatheridiidae, Gregory and Simpson (1926) stated that *Didelphodus* might belong in that group, and I still later (Simpson, 1928) gave in somewhat more detail the reasons for this tentative assignment.

*Gelastops* of the present fauna is sufficiently close to *Didelphodus* to warrant their tentative collocation in one subfamily but, as brought out more fully in describing *Gelastops*, this is not certain. In any case *Gelastops* is poorly known and adds little to evidence for the affinities of this group. Its more aberrant premolar structure, still more striking in the probably allied *Acmeodon*, does to some extent argue against close affinities with the much more primitive Cretaceous forms but this may merely indicate an incipient line of specialization within the Deltatheridiidae. The data do not warrant a more positive conclusion. On present evidence it seems well to retain Matthew's subfamily Didelphodontinae, for *Didelphodus*, *Gelastops*, *Acmeodon*, and probably *Phenacops*. This necessitates the proposal of a new subfamily Deltatheridiinae, defined, among other characters, by the less progressive premolars, less separated paracone and metacone, and narrower talonids.

#### Genus GELASTOPS Simpson

*Gelastops* SIMPSON, 1935d, p. 227.

*Emperodon* SIMPSON, 1935d, p. 229.

*Type*.—*Gelastops parvus* Simpson.

*Type of Emperodon*.—*Emperodon acmeodontoides* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Mont.

*Diagnosis*.—Canine large and erect.  $P_4$  intermediate in structure between *Didelphodus* and *Acmeodon*, with paraconid high on crown, metaconid nearly as high as protoconid and partly confluent with latter, a vertical crest descending posteriorly from the metaconid and another from the protoconid, and a small, bicuspid, basined talonid. Molars leptictid or didelphodontine, paraconids large and more internal than in *Prodiacodon* or similar leptictids, trigonids elevated, that

of  $M_1$  large relative to talonid and those of  $M_{2-3}$  compressed antero-posteriorly.  $M_2$  and particularly  $M_3$  reduced relative to  $M_1$ , heel of  $M_3$  much reduced but with projecting hypoconulid.

*Discussion.*—By an unfortunate chance the National Museum material of this unusual genus does not include associated  $P_4$  and  $M_1$ . Since  $P_4$  seems clearly related to *Acmeodon*, while  $M_1$  seems just as clearly related to *Didelphodus*, and since the possibility of relationship between *Acmeodon* and *Didelphodus* had never been suggested, I was led to believe that two different animals were represented, one related to each of these genera. Specimens collected since this manuscript was first completed show that the  $P_4$  supposedly characteristic of *Emperodon* and the  $M_1$  supposedly characteristic of *Gelastops* really belonged to the same animal and this has made possible a last-minute correction in the present work.

There is little doubt that *Gelastops* is related to *Acmeodon*, although it is, on the whole, more primitive in structure. It had the anterior premolars less reduced than in the latter.  $P_4$  is superficially quite different in the two genera, but the differences appear to be modifications of the same fundamental structure, which is unlike that of any other genera known to me. In *Gelastops* the paraconid is larger and more internal and the metaconid is distinct, but the latter is probably represented in *Acmeodon* by the cuspule on the posterointernal crest descending from the protoconid, in which case the distinction is the relatively minor one that in *Gelastops* this cuspule is merely more emphasized and shifted slightly anteriorly. The peculiar protostylid is larger in *Acmeodon* but is also present in *Gelastops*. In *Acmeodon* the two crests run into the talonid rim and the valley between them into the talonid basin in such a way that the talonid is poorly differentiated, while in *Gelastops* the talonid is well set off by notches, but the parts seem to be entirely homologous in the two cases. The large and internal paraconid and talonid markedly narrower than trigonid, which so strikingly separate *Acmeodon* from the Leptictidae, are developed in almost exactly the same way in *Gelastops*.

On the other hand, there is also good evidence for the relationship of *Gelastops* to *Didelphodus*. The general aspect of the jaw, canine, and cheek dentition is much the same in the two genera. In *Gelastops*  $P_1$  is probably more reduced and  $P_{2-4}$  more elevated.  $P_4$  is definitely more specialized in *Gelastops* than in *Didelphodus*, having a higher crown, more elevated (but little larger) paraconid, larger and much more elevated metaconid, and more prominent posterior crest on the metaconid. This crest is, however, distinctly present in *Didelphodus* and in general all the structural features seem to correspond in the two genera, the differences involving only relative proportions and prominence of the various parts.

The lower molars of *Gelastops* so closely resemble those of *Didelphodus* as to make a hypothesis of relationship most reasonable. The only really clear difference is the greater elevation of the trigonids in *Gelastops* and this is not extreme. The upper molar mentioned below also adds to the evidence, but the reference is not certain.

*Gelastops* thus resembles both *Acmeodon* and *Didelphodus* and is structurally almost intermediate between the two. Without producing absolute proof, it strongly suggests that the three genera *Didelphodon*, *Gelastops*, and *Acmeodon* belong to a natural group, and they are here tentatively recognized as constituting the subfamily Didelphodontinae. There are still difficulties in the way of this interpretation that perhaps can be resolved only by the discovery of upper dentitions of *Gelastops* and *Acmeodon*. The outstanding difficulty is that the series *Didelphodus-Gelastops-Acmeodon* is an excellent structural sequence in that order, on the basis of the parts now known in all, but that the most primitive genus, *Didelphodus*, is the latest in time, a relationship that is fully possible but that requires better evidence for definitive acceptance.

#### GELASTOPS PARCUS Simpson

FIGURES 12, 13

*Gelastops parcus* SIMPSON, 1935d, p. 227.

*Emperodon acmeodontoides* SIMPSON, 1935d, p. 229.

*Type*.—U.S.N.M. no. 6148, right lower jaw with canine,  $M_1$ ,  $M_3$ , and alveoli. Collected by A. C. Silberling.

*Type of* *Emperodon acmeodontoides*.—U.S.N.M. no. 9850, right lower jaw with  $P_4$ ,  $M_2$ , and part of  $P_3$ . Collected by A. C. Silberling.

*Horizon and locality*.—Type probably from Silberling Quarry,<sup>52</sup> other specimens from Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus. Measurements in table 22.

*Remarks*.—Besides the type and that of the synonym, there are two referred specimens from the Gidley Quarry in the National Museum collection: U.S.N.M. no. 9601, a right lower jaw with  $M_{2-3}$  and alveoli, and U.S.N.M. no. 9446, a right lower jaw with  $M_{2-3}$ .

From the alveoli it appears that a reduced  $P_1$  was present; this tooth is absent in *Acmeodon* and unreduced in *Didelphodus*.  $P_{2-3}$  were present and each had two well-separated roots. The structure of  $P_4$  has already been sufficiently described except to note that the protoconid tip bends outward (labially) in a peculiar way, approach-

<sup>52</sup> There is some inconsistency in the available records. It is certain that the type is from the Fort Union No. 2, and from its preservation it must be from one of these two quarries, but some error or omission had been made in recording the field number. Being collected in 1908, it is more likely to be from the Silberling Quarry.



ing *Acmeodon*, its outer wall looking as if it had been plastically deformed by pressing the apex outward. Except for details in the generic diagnosis or evident from the measurements, the lower molars so closely resemble those of *Didelphodus absarokae*, described by Matthew (1918), that further description of them is not necessary.

There is a single left M<sup>2</sup>, U.S.N.M. no. 9554, from the Gidley Quarry, that may belong to this species, although it differs more markedly from *Didelphodus absarokae* than do the lower molars. It is remarkably short and wide, or extremely transverse, and further differs from *Didelphodus* in the great extension of the parastyle spur, the slightly more external position of paracone and metacone, and the vestigial character of the metaconule. It resembles *Didelphodus* in other respects, such as the emarginate outer border, shelf-like meta-

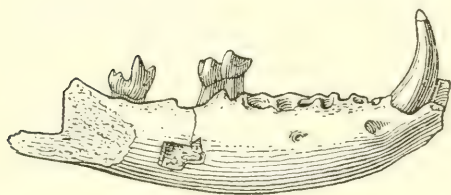


FIGURE 12.—*Gelastops parvus* Simpson, U.S.N.M. no. 6148: Right lower jaw, external view. Twice natural size.

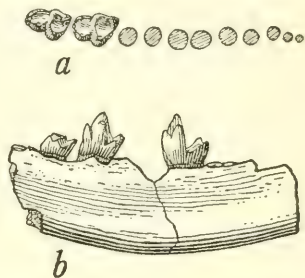


FIGURE 13.—*Gelastops parvus* Simpson:  
a, Crown view of right lower teeth  
and alveoli, U.S.N.M. no. 9601; b,  
internal view of right lower jaw, U.S.  
N.M. no. 9850. Twice natural size.

stylar extension, connate bases of paracone and metacone, and entire absence of hypocone or of anterior or posterior cingula. The transverse extension and the reduction of the metaconule are, furthermore, *Didelphodus*-like but here more extreme and the nonmarginal position of paracone and metacone are also *Didelphodus*-like but less pronounced.

TABLE 22.—Measurements of individual specimens of *Gelastops parvus*.

[illegible]

## Family LEPTICTIDAE Gill, 1872

Unlike many of the Paleocene and Lower Eocene groups referred to the Insectivora, the Leptictidae are Insectivora *sensu stricto*. That is, they are not merely primitive forms that are presumed to have been derived from an undifferentiated insectivore stock and that do not enter well into any other order, but are definitely insectivores in a special sense, clearly related to recent insectivores. Their affinities seem to be with the erinaceoids, although here they constitute an extinct side line, not ancestral to the true Erinaceidae. More exact elucidation of their affinities depends on full analysis of the characters of the Oligocene forms, which are known from nearly complete skeletons but have never been adequately studied.

Matthew (1918) has pointed out that there is a group of genera undoubtedly leptictid (now about nine genera) and that in addition to these there are several diverse genera placed here without much positive evidence but in default of other indications. *Didelphodus*, *Phenacops*, and *Acmeodon*, then placed here by Matthew, are now

TABLE 23.—Comparison of lower dentition of five genera of Paleocene Leptictidae

| Genus                  | Canine    | P <sub>4</sub>                                                                                                                                                              | Trigonids                                                        | Molar paraconids                                                                | M <sub>3</sub> talonid        |
|------------------------|-----------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------|---------------------------------------------------------------------------------|-------------------------------|
| <i>Diacodon</i> .....  | Small..   | With sharp, low, median paraconid. Protoconid and metaconid opposite and nearly equal. Heel basined, with 3 cusps, hypoconid largest and nearly confluent with hypoconulid. | Trigonids of P <sub>4</sub> -M <sub>3</sub> moderately elevated. | Lower than other trigonid cusps, small, submedian.                              | Elongate.                     |
| <i>Prodiacodon</i> ... | Large..   | With trigonid similar to <i>Diacodon</i> . Talonid with hypoconid relatively less dominant, hypoconulid more separate, sometimes with 4 distinct talonid cusps.             | Trigonids of P <sub>4</sub> -M <sub>3</sub> strongly elevated.   | About as in <i>Diacodon</i> .                                                   | About as in <i>Diacodon</i> . |
| <i>Leptacodon</i> .... | Large..   | Closely similar to <i>Diacodon</i> , but metaconid smaller, usually posterointernal to protoconid. Talonid small.                                                           | Little elevated..                                                | Nearly internal, otherwise more like <i>Diacodon</i> .                          | Short.                        |
| <i>Myrmecoboides</i> . | Moderate. | Elongate, trigonid similar to <i>Diacodon</i> . Talonid long, narrow, basined, without distinct hypoconulid, entoconid about equal to hypoconid.                            | Moderately elevated.                                             | Small but nearly as high as metaconids, fully internal, fusing with metaconids. | Very elongate.                |
| <i>Xenacodon</i> ..... | Small..   | With small basal paraconid, large metaconid. Talonid very short, not basined.                                                                                               | -----do-----                                                     | About intermediate between <i>Diacodon</i> and <i>Leptacodon</i> .              | Short, strongly reduced.      |

tentatively removed to the Deltatheridiidae. The genus of most doubtful affinities still retained in this family is *Xenacodon* Matthew and Granger, of the Tiffany.

The more positively leptictid genera *Diacodon*, *Prodiacodon*, *Leptacodon*, and *Myrmecoboides* also occur in the Paleocene, the last three being represented in this fauna. Table 23 shows some of the more striking distinctions in the lower dentitions of the five genera recorded from the Paleocene.

Of these genera, *Diacodon*, *Prodiacodon*, and *Leptacodon* are typical leptictids and are evidently very closely allied, to such a point that they are rather difficult to distinguish. *Myrmecoboides* seems to be a true leptictid but is highly distinctive and perhaps not closely related to any of the more typical genera. *Xenacodon* is a distinctive but poorly known and rather dubious form.

Genus **PRODIACODON** Matthew, 1929

**PRODIACODON CONCORDIARCENSIS** Simpson

FIGURE 14

*Prodiacodon concordiarzensis* SIMPSON, 1935d, p. 228.

*Type*.—U.S.N.M. no. 9637, left lower jaw with  $P_2$ ,  $P_4$ ,  $M_3$ , and alveoli. Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

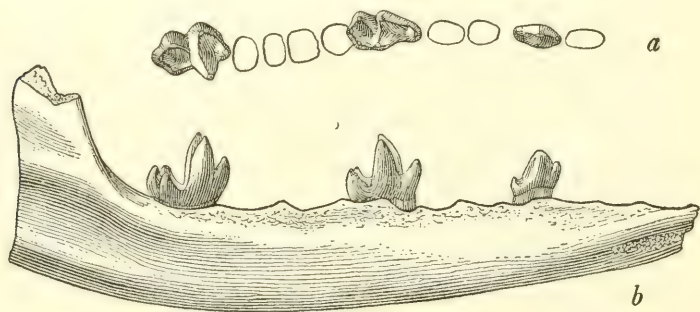


FIGURE 14.—*Prodiacodon concordiarzensis* Simpson, U.S.N.M. no. 9637, left lower jaw: *a*, Crown view; *b*, internal view. Five times natural size.

*Diagnosis*.—Much smaller than *Prodiacodon puercensis*.  $P_4$  with paraconid more secant and projecting more anteriorly, talonid with three conical cusps, hypoconid largest and entoconid smallest.  $M_3$  with trigonid more slender and markedly elevated, talonid less elongate, with three subequal cusps.

*Remarks*.— $P_2$  has a high but small paraconid and low posterior cuspule. The horizontal ramus is very long and slender, and the anterior teeth were evidently procumbent.



This delicate species differs so much from *Prodiacodon puercensis* that the generic reference is not at all certain, but the only alternative would be erecting a new genus, which is highly undesirable at present. The present form is apparently a typical leptictid, peculiar only in minute details, and as close to *Prodiacodon* as to any other defined genus. It is almost equally close to *Leptacodon*, but its reference there would make the generic definitions almost impossible to frame adequately.

The type is the only known specimen. Its dimensions are as follows: Length  $P_2$ , 1.3; width  $P_2$ , 0.5; length  $P_4$ , 2.0; width  $P_4$ , 1.1; length  $M_3$ , 1.9; width  $M_3$ , 1.2.

### Genus LEPTACODON Matthew and Granger, 1921

#### LEPTACODON LADAE Simpson

#### FIGURE 15

*Leptacodon ladae* SIMPSON, 1935d, p. 228.

*Type*.—U.S.N.M. no. 9640, right lower jaw with  $P_4$ – $M_3$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

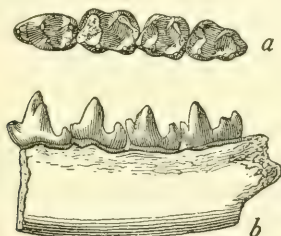


FIGURE 15.—*Leptacodon ladae* Simpson, U.S.N.M. no. 9640, right lower jaw: a, Crown view; b, internal view. Five times natural size.



FIGURE 16.—*Leptacodon munusculum* Simpson, U.S.N.M. no. 9819, left lower jaw: a, Crown view; b, internal view. Five times natural size.

*Diagnosis*.—Slightly larger than *L. tener* or *L. packi* and slightly smaller than *L. siegfriedti*, structurally closer to the former two species (subgenus *Leptacodon*) than to the latter (subgenus *Leipsanolestes*).  $P_4$  elongate, paraconid median, metaconid very small but in the same position as in *L. tener*, talonid as in that species. Molar paraconids smaller than in *L. tener* but distinct and internal. Hypoconulids of  $M_{1-3}$  more projecting than in *L. tener*. Talonid of  $M_3$  more elongate and entoconid smaller.

*Remarks*.—This species is referable to *Leptacodon* with very little doubt. Although fairly common in the Gidley Quarry, the specimens are all very fragmentary, and they add nothing to knowledge of the genus beyond making it a little more varied.

The dimensions of the type are as follows: Length  $P_4$ , 1.4; width  $P_4$ , 1.0; length  $M_1$ , 1.5; width  $M_1$ , 1.2; length  $M_2$ , 1.4; width  $M_2$ , 1.3; length  $M_3$ , 1.5; width  $M_3$ , 1.1.

The available numerical data on the whole sample are given in table 24.

TABLE 24.—Numerical data on specimens of *Leptacodon ladae*

| Variate          | N | R       | M               | $\sigma$        | V              |
|------------------|---|---------|-----------------|-----------------|----------------|
| $LP_4$ -----     | 5 | 1.4—1.6 | 1.48            |                 |                |
| $WP_4$ -----     | 5 | 0.8—1.0 | 0.90            |                 |                |
| $LM_1$ -----     | 7 | 1.4—1.6 | $1.53 \pm 0.03$ | $0.07 \pm 0.02$ | $4.6 \pm 1.2$  |
| $WM_1$ -----     | 6 | 1.0—1.3 | $1.17 \pm 0.04$ | $0.09 \pm 0.03$ | $8.1 \pm 2.3$  |
| $LM_2$ -----     | 9 | 1.3—1.6 | $1.43 \pm 0.03$ | $0.08 \pm 0.02$ | $5.7 \pm 1.3$  |
| $WM_2$ -----     | 8 | 0.9—1.4 | $1.20 \pm 0.05$ | $0.14 \pm 0.04$ | $11.7 \pm 2.9$ |
| $LM_3$ -----     | 8 | 1.4—1.6 | $1.51 \pm 0.02$ | $0.06 \pm 0.02$ | $4.0 \pm 1.0$  |
| $WM_3$ -----     | 7 | 1.0—1.2 | $1.09 \pm 0.02$ | $0.06 \pm 0.02$ | $5.9 \pm 1.6$  |
| $LM_{1-3}$ ----- | 3 | 4.5—4.7 | 4.57            |                 |                |

The two available specimens of *L. tener* are at or slightly below the observed lower limits for *L. ladae* in all molar dimensions. The deviations of the four available dimensions of the type of *L. tener* from the means of *L. ladae*, divided by the corresponding standard deviations of the latter ( $d/\sigma$ ) are as follows:

$$LM_1: -6.1$$

$$LM_2: -4.0$$

$$WM_1: -5.0$$

$$WM_2: -2.9$$

The size difference, slight as it is, thus appears to be significant. Individual measurements of *L. packi* are not available, but that species is very close to *L. tener* in size, hence probably also significantly smaller than *L. ladae*.

#### LEPTACODON MUNUSCULUM Simpson

##### FIGURE 16

*Leptacodon munusculum* SIMPSON, 1935d, p. 228.

*Type*.—U.S.N.M. no. 9819, left lower jaw with  $M_1$  and  $M_3$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.— $M_1$  of about the same size as in *L. tener*,  $M_3$  more reduced.<sup>53</sup> Paraconids smaller and more strictly internal. Talonid of  $M_3$  relatively narrower.

*Remarks*.—This poorly known species is the smallest mammal in the collection and is one of the smallest mammals known. It is

<sup>53</sup> The original diagnosis says "Slightly smaller than *Leptacodon tener*", which was probably true of the dentition as a whole and perhaps of the animal, but  $M_1$  is as large as in *L. tener*.

almost certainly referable to this genus but is shown to be a distinctive species even from the one very fragmentary specimen available.  $M_1$  is 1.2 and  $M_3$  1.1 mm in length. The comparison with *L. ladae* by  $d/\sigma$  is thus as follows:

LM<sub>1</sub>:4.7

LM<sub>3</sub>:6.8

The ratio LM<sub>1</sub>/LM<sub>3</sub> compares as follows:

*L. tener* (referred specimen):0.86.

*L. ladae* (three specimens):1.00–1.07, mean 1.05.

*L. minusculum*:1.09.

$M_3$  is thus more reduced in *L. ladae* and in *L. minusculum* than in *L. tener*. The difference between *L. minusculum* and *L. ladae* may be, but is not shown to be, significant.

### Genus MYRMECOBOIDES Gidley

*Myrmecoboides* GIDLEY, 1915, p. 395.

*Type*.—*Myrmecoboides montanensis* Gidley.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Canine of moderate size. Premolars well spaced.  $P_4$  elongate, with strong but low, median paraconid, metaconid well separated and nearly as high as protoconid, talonid long and narrow with small, subequal hypoconid and entoconid and hypoconulid barely suggested. Molars, particularly  $M_3$ , with long talonids and with moderately elevated trigonids. Paraconids smaller than metaconids but nearly as high and partly connate, so that paraconid and metaconid together form a twinned apex that is higher than the protoconid.

*Remarks*.—Gidley stated that the name *Myrmecoboides* was "given to the ancient form on account of its likeness to *Myrmecobius* rather than as a positive assumption of real relationship." He did, however, state that the genus was marsupialian and probably related to the Myrmecobiidae, and he went into much detail regarding its bearing on marsupial evolution. Abel (1919) placed *Myrmecoboides* in the Myrmecobiidae. Osgood (1921) stated that *Myrmecoboides* might well be ancestral to *Caenolestes*, if it was a marsupial. Schlosser (1923) classified it in the Myrmecobiidae but noted that it might not be marsupial. Longman (1924) gave a résumé of Gidley's view, stating (as had Gidley) that the resemblances to *Myrmecobius* were suggestive but not conclusive. Matthew (1916) had, however, quickly pointed out that the characters of *Myrmecoboides* are not myrmecoboid or marsupial, but leptictid and placental. Gidley also came to accept this conclusion (personal communication) but apparently did not publish this fact. Students of Paleocene mammals have long realized that *Myrmecoboides* cannot be a marsupial, but aside from Matthew's brief statement, which has been overlooked by almost all later com-



mentators, the evidence has not been clearly stated in publication and Gidley's abandoned view is becoming entrenched in the literature. It is therefore necessary to consider it here.

Gidley did not explicitly discuss the evidence for referring *Myrmecoboides* to the Marsupialia. It is clear that the reference was based almost entirely on the molariform character of the fourth cheek tooth, and in part simply on a general resemblance to the one marsupial genus *Myrmecobius*. Gidley mentions the three possibilities regarding the molariform tooth: that it is a true molar, that it is a deciduous molar, and that it is a true premolar. He cites the narrower crown, smaller talonid, and large, anteriorly directed paraconid as seemingly precluding the possibility that the tooth is a true molar. This evidence is valid, and to it may be added (as first pointed out by Matthew) the fact that the protrusion and wear of the tooth definitely prove that it was erupted long after the following tooth, which could not be true of a first molar. Gidley states that the very complex structure in comparison with  $P_3$  opposes the supposition that this is  $P_4$  and supports his conclusion that it is  $dm_4$ , retained in the adult dentition. But the relative time of eruption, as first shown by Matthew, is impossible for  $dm_4$ , which in all known mammals is erupted before  $M_1$  rather than long after, as the tooth in question is in *Myrmecoboides*. Furthermore, the fourth cheek tooth in marsupials, whether it be  $M_1$  or  $dm_4$ , is erupted before the following tooth or at almost the same time. Gidley also seems to have overlooked, momentarily, the fact well known to him that in the Leptictidae and some other unquestionable placentals  $P_4$  is characteristically as molariform as this tooth, or more so, even though  $P_3$  may be as simple as in *Myrmecoboides*. It may be concluded, and Gidley also did conclude on more mature deliberation, that this is certainly  $P_4$ , and hence that its evidence is entirely opposed to marsupial and in favor of placental affinities for the genus.

Gidley analyzed all the resemblances to and differences from *Myrmecobius*. The only resemblances that could be supposed to carry much weight are the spacing of the premolars and the elevation of the internal cusps of the molars. These characters also do occur in placentals and are highly aberrant among marsupials. These, and all the other lesser points of resemblance, would perhaps tend to link *Myrmecoboides* to *Myrmecobius* if the former were otherwise proved to be a marsupial, but they have no value as to the primary question of showing it to be marsupial. There are indeed profound differences between the fossil and *Myrmecobius*. Gidley recognized these but concluded that degeneration could lead to this great transformation, which is true but is not evidence that it did so. On the other hand, *Myrmecoboides* has the basic and diagnostic characters of the Leptictidae, and the *Myrmecobius*-like characters can only be interpreted as superficial, aberrant, habitus characters bringing about a slight degree of convergence.

The fact that *Myrmecoboides* is not a marsupial obviously deprives it of any bearing on whether the fourth cheek tooth of marsupials is  $dm_4$  or  $M_1$ , a question that Gidley properly discussed when under a misapprehension as to the affinities of the genus. It also removes this much support from Gidley's thesis, which was, however, also supported by other evidence, that the Australian families were differentiated outside Australia and at a very early date.<sup>54</sup>

Among the Leptictidae, *Myrmecoboides* is aberrant and does not belong with such typical genera as *Diacodon* or *Leptacodon*, although its less direct relationship with them is highly probable.

#### MYRMECOBOIDES MONTANENSIS Gidley

FIGURES 17, 18

*Myrmecoboides montanensis* GIDLEY, 1915, p. 395.

*Type*.—U.S.N.M. no. 8037, left lower jaw with canine and  $P_1$ – $M_3$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus. Dimensions below.

*Remarks*.—Gidley (1915) has accurately described the lower dentition, and the slightly different emphasis demanded by transfer to this family is supplied by the revised generic diagnosis. The second specimen mentioned by Gidley is U.S.N.M. no. 9418, which has only  $M_{1-2}$  and these so worn that the cusp structure cannot be made out.

U.S.N.M. no. 9552 is a right upper jaw with  $P^4$ – $M^3$  that is so well suited to be the upper dentition of *Myrmecoboides montanensis*, and not of any other known species in the fauna, that it may be referred here. Dr. Gidley has noted that this is probably the upper dentition of *Myrmecoboides*—further evidence of his later recognition of the affinities of the genus, for this upper jaw is entirely leptictid in character and does not at all resemble *Myrmecobius*. These upper teeth are very close to those of *Prodiacodon* throughout.  $P^4$  seems to have had the paracone and metacone better separated in *Myrmecoboides*, but is imperfect in this region.  $M^1$  has the external shelf more pronounced, the parastylar and metastylar lobes more projecting, a deep

<sup>54</sup> When Gidley wrote, it was a reasonable *a priori* assumption that diverse marsupials would be the micro-faunal elements most likely to appear in the Paleocene, although subsequent discovery has shown this not to be the case. He was inevitably predisposed toward this view (as was also Matthew and as were other contemporaneous students), and his preliminary note on *Myrmecoboides* suffered from this preconception. It is further exemplified by his manuscript notes on several other placental genera labeled as "Marsupial No. 1" and so on; it has not seemed necessary to cite this first impression in each case, as Dr. Gidley would certainly have abandoned it before completing his studies. Dr. Gidley also had a strong and more personal predisposition, strikingly exemplified in the *Myrmecoboides* paper, to believe that the modern mammalian families were of extremely remote origin. This is a legitimate thesis, and the erroneous nature of part of the supposed evidence does not remove the possibility or vitiate Gidley's whole argument. His conclusion unquestionably contains an important truth, but I believe, apparently with the consensus of recent students, that he overemphasized its importance and extent.

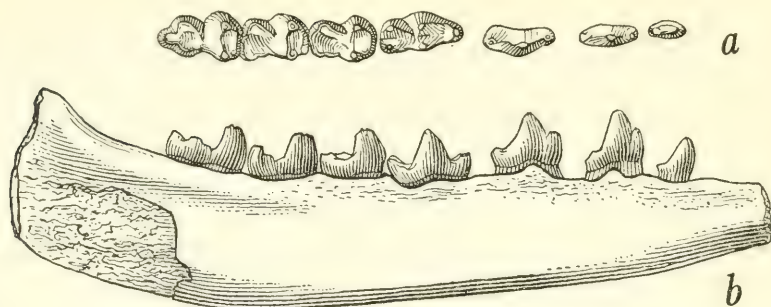


FIGURE 17.—*Myrmecoboides montanensis* Gidley, U.S.N.M. no. 8037, left lower jaw: a, Crown view; b, internal view. Four times natural size.

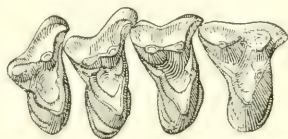


FIGURE 18.—*Myrmecoboides montanensis* Gidley, U.S.N.M. no. 9552, right upper P<sup>4</sup>-M<sup>3</sup>, crown view. Four times natural size.

median notch in the external border, and the hypocone more internal. M<sup>2</sup> has the outer portion analogously modified, but this is less distinctive from *Prodiacodon* than is M<sup>1</sup>. M<sup>3</sup> is of almost identical structure in the two genera.

TABLE 25.—Measurements (in mm) of the type and of the referred upper jaw of *Myrmecoboides montanensis*

| P <sub>1</sub> |     | P <sub>2</sub> |     | P <sub>3</sub> |     | P <sub>4</sub> |     | M <sub>1</sub> |     | M <sub>2</sub> |     | M <sub>3</sub> |     | P <sup>4</sup> |     | M <sup>1</sup> |     | M <sup>2</sup> |     | M <sup>3</sup> |     |
|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
| L              | W   | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   |
| 1.1            | 0.6 | 1.8            | 0.8 | 2.3            | 0.9 | 2.7            | 1.3 | 2.4            | 1.5 | 2.3            | 1.5 | 2.6            | 1.5 | 2.6            | 3.3 | 2.3            | 3.7 | 2.4            | 3.8 | 2.0            | 3.7 |

### Family NYCTITHERIIDAE Simpson, 1928

This family was established to include a number of rather poorly known Paleocene and Eocene genera, all represented by species of small or minute size, that probably represent a single varied group and that seem to be primitive shrewlike insectivores, without any of the specializations characteristic of the true shrews. In this respect the dentition is molelike rather than shrewlike, but there is no evidence of definitely talpid specializations. As Matthew (1909) has pointed out (in other words), speaking of Eocene genera that I have since placed in this family, they seem to combine all the most primitive characters of the moles and the shrews. To this extent the evi-



dence suggests an undifferentiated group from which these late insectivores arose, but annectant types are lacking and knowledge is too incomplete to test this hypothesis adequately. Matthew (1918) has also pointed out that *Nyctitherium* itself may be a chiropteran, and this may be true of the whole group, or it may be a primitive complex allied or ancestral to all three groups, Talpoidea, Soricoida, and Chiroptera, although there is reason to suppose that these three groups were already distinct before the end of the Paleocene. It is likewise possible that two or all three of these groups had acquired their skeletal specializations but not their dental characters in the Paleocene and that the nyctitheriids are an artificial assemblage based on dental resemblance only. Despite this possibility, it seems most practical to continue to associate them in this family until some broader basis for classification becomes available.

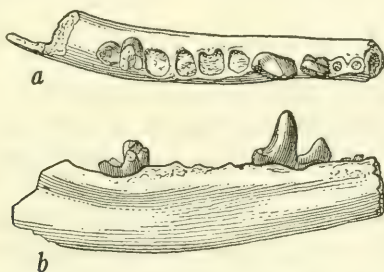


FIGURE 19.—*Stilpnodon simplicidens* Simpson, U.S.N.M. no 9629, left lower jaw: a, Crown view; b, internal view. Five times natural size.

In the National Museum collection only one nyctitheriid specimen is available, but it represents a distinctive genus, *Stilpnodon*. It is not very close to any other known genus, and its reference to the family is not certainly established, but it is most conveniently placed here. It shares with *Leptacodon munusculum* the distinction of being the smallest known mammal of this fauna.

#### Genus STILPNODON Simpson

*Stilpnodon* SIMPSON, 1935d, p. 229.

*Type*.—*Stilpnodon simplicidens* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Mont.

*Diagnosis*.— $P_4$  with very high, slender main cusp, minute rudimentary anterior basal caspule, no metaconid, simple nonbasined talonid with one cuspsule.  $M_3$  reduced, with distinct, low, nearly median paraconid, trigonid erect and moderately elevated above talonid, protoconid large, trigonid nearly as long as talonid, talonid short and much narrower than trigonid.

## STILPNODON SIMPLICIDENS Simpson

FIGURE 19

*Stilpnodon simplicidens* SIMPSON, 1935d, p. 229.

*Type*.—U.S.N.M. no. 9629, left lower jaw with  $P_{3-4}$ ,  $M_3$ , and alveoli.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus.  $P_4$  length, 1.0 mm.  $M_3$  length, 1.2 mm.

*Remarks*.— $P_3$  is very simple, without anterior basal cuspule and with the sloping heel not forming a distinct cusp. From its roots,  $P_2$  was of about the same size as  $P_3$ . The posterior mental foramen is beneath the anterior root of  $P_4$ .

## Family PANTOLESTIDAE Cope, 1884

In his Bridger memoir Matthew (1909) united various genera previously widely scattered in the system and placed them in the Pantolestidae. From a study of *Pantolestes*, a relatively specialized but well-known Middle Eocene genus, he showed that at least the typical members of the family have basic insectivore characters, overlain by peculiar specializations not closely paralleled in recent insectivores. He interpreted the majority of these specializations in *Pantolestes* as adaptations to aquatic, or to amphibious, life. At that time he pointed out that *Palaeosinopa*, then known from the Lower Eocene, is closely related to *Pantolestes* and that *Pentacodon*, of the Middle Paleocene, might tentatively be placed in this family. In 1918 Matthew revised and carefully described the Lower Eocene *Palaeosinopa*, again emphasizing its close relationship to *Pantolestes*, and reviewed the evidence for reference of these genera to the Insectivora. This evidence, which still appears to be adequate for such a conclusion is, in briefest possible outline, that the pantolestid dentition is, indeed, more creodontlike than like any recent insectivore but is also closely similar to the unquestionably insectivore leptictids, and that numerous characters of skull and skeleton (especially the astragalus) are quite unlike any known creodonts or other carnivores but do resemble the Leptictidae and other Insectivora. A special point of the evidence (singled out by Schlosser, see Matthew, 1918, for undue emphasis) is the position of the posterior mental foramen beneath  $M_1$ , a character known only in Insectivora, although not characterizing all members of that order.

Various fragments suggested the presence of this family in the Upper Paleocene (e. g., Simpson, 1927), and Jepsen (1930a) referred a

partial jaw from the Middle Paleocene to *Palaeosinopa*. I have described a genus, *Bessoeceter*, from the Upper Paleocene (Simpson, 1936b). The present fauna includes a distinctive species that seems surely to be closely allied to or in the *Palaeosinopa*-*Pantolestes* line and is tentatively referred to *Bessoeceter*, thus definitely projecting the typical pantolestid phylum back into the Middle Paleocene. It also includes in *Aphronorus* an ally of *Pentacodon*, represented by much better material than is that Torrejon genus and much improving our knowledge of this small group.

The probable relationship of *Pentacodon* and *Aphronorus*, on one hand, and *Bessoeceter*, *Palaeosinopa*, and *Pantolestes*, on the other, is confirmed and strengthened by the present evidence. In both the lower jaw has a large semiprocumbent canine followed by three small elongate premolars of similar pattern in the two groups and then by a relatively enlarged premolar, the pattern of which is, however, unlike in the two lines. The molars, upper and lower, are of almost exactly similar pattern, with only such minute differences as are encountered among very closely allied genera. The posterior mental foramen is beneath  $M_1$  in both cases and the other known osteological characters, although few and not very distinctive, are generally similar.

The only characters opposing such relationships are those of  $P^4$ , which are more and differently specialized in *Pentacodon* and *Aphronorus* than in *Bessoeceter* or even the much later genus *Pantolestes*. These marked differences do not seem to exclude a family relationship, but they do show that two divergent and sharply defined groups are included, especially when the distribution of the various genera is taken into account. In the present state of knowledge it seems convenient to formalize this distinction by placing the known genera in two subfamilies, the Pantolestinae with *Bessoeceter*, *Pantolestes*, *Palaeosinopa*, and perhaps some less well known forms, and the Pentacodontinae with *Pentacodon* and *Aphronorus*. For the present these are immediately and adequately distinguishable from the characters of  $P^4$  as given in the diagnosis below.

#### PANTOLESTINAE, new subfamily

*Type*.—*Pantolestes* Cope, 1872.

*Distribution*.—Middle Paleocene to Middle Eocene, North America. Lower Eocene, Europe.

*Diagnosis*.— $P^4$  relatively little enlarged.  $P_4$  compressed, no metaconid, semishearing, heel essentially unicuspid and little or not basined.  $P^4$  with compressed amphicone, no metacone, low, sharp styles, small protocone without cingula.



Genus **BESSOECETOR** Simpson

*Bessoecetor* SIMPSON, 1936b, p. 9.

*Type*.—*Bessoecetor thomsoni* Simpson.

*Distribution*.—Middle and Upper Paleocene, Fort Union, Montana.

This genus was based on an unusually good suite of specimens from the Scarritt Quarry. It is evidently very closely allied to *Palaeosinopa* but seems to be slightly more primitive in several respects. The species *Palaeosinopa diluculi*, previously recorded from the present fauna (Simpson, 1935d, p. 230) appears to be more nearly related to *Bessoecetor* and may be provisionally placed in that genus, although it is too poorly known to reveal all the desired generic characters. Most of the characters in which it differs from Lower Eocene species of *Palaeosinopa* and which were therefore given as specific characters in the original diagnosis are now shown by the fine material of *Bessoecetor*



FIGURE 20.—*Bessoecetor diluculi* (Simpson), U.S.N.M. no. 9810, with parts in outline added from U.S.N.M. nos. 9312 and 9539, left lower jaw: a, Crown view; b, internal view. Three times natural size.

*thomsoni* to be generic characters of *Bessoecetor*. This includes, most notably, the strongly trenchant  $P_4$  with large anterior basal cusp and incipient basining of talonid, the relatively small expansion of the hypocone shelves, and the less reduced  $M^3$ . The Middle Paleocene form also has the sharply distinguished molar talonid cusps characteristic of *Bessoecetor*.

**BESSEOECETOR DILUCULI** (Simpson)

## FIGURES 20, 21

*Palaeosinopa diluculi* SIMPSON, 1935d, p. 230.

*Type*.—U.S.N.M. no. 9810, left lower jaw with  $P_4$ – $M_2$ . Collected by A. C. Silberling.

*Paratype*.—U.S.N.M. no. 9553, left upper jaw with  $P^4$ – $M^3$  (somewhat broken). Collected by A. C. Silberling.

*Horizon and locality*.—Gidley and Silberling Quarries, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

**Diagnosis.**— $P_4$  and  $M_{2-3}$  significantly larger than in *B. thomsoni*,  $M_1$  about same size. Heel of  $P_4$  relatively larger, talonid of  $M_3$  more elongate. Amphicone of  $P^4$  more compressed.

**Remarks.**—The dentition is closely similar to that of *B. thomsoni*, fully described elsewhere (Simpson, 1936b).

TABLE 26.—*Dentition measurements (in mm) of Bessocetor diluculi*

| U.S.N.M. no. | $P_4$ |       | $M_1$ |       | $M_2$ |       | $M_3$ |       |
|--------------|-------|-------|-------|-------|-------|-------|-------|-------|
|              | L     | W     | L     | W     | L     | W     | L     | W     |
| 9810-----    | ----- | 1.3   | 2.4   | 1.7   | 2.5   | 2.0   | 3.3   | 2.3   |
| 9312-----    | ----- | ----- | ----- | ----- | 2.6   | 2.2   |       |       |
| 9442-----    | ----- | 1.4   | 2.3   | 1.7   | 2.7   | 2.0   |       |       |
| 9539-----    | 3.2   | 1.3   | 2.7   | 1.8   | ----- | ----- | ----- | ----- |

| U.S.N.M. no. | $P^4$ |       | $M^1$ |       | $M^2$ |     | $M^3$ |     |
|--------------|-------|-------|-------|-------|-------|-----|-------|-----|
|              | L     | W     | L     | W     | L     | W   | L     | W   |
| 9553-----    | ----- | ----- | 2.7   | 3.4   | 2.8   | 3.8 | 2.0   | 3.5 |
| 9585-----    | 2.6   | ----- | 2.5   | ----- | 2.6   | 3.5 |       |     |

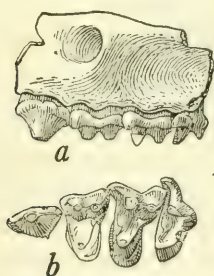


FIGURE 21.—*Bessocetor diluculi* (Simpson), U.S. N.M. no. 9553, with part in outline added from U.S.N.M. no. 9585, left upper jaw: a, External view; b, crown view. Three times natural size.

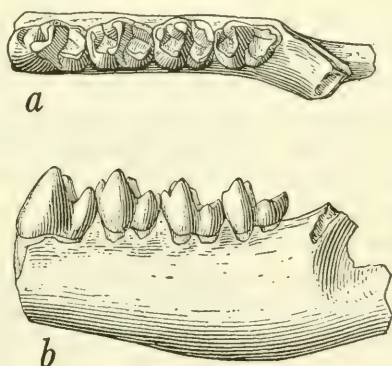


FIGURE 22.—*Aphronorus fraudator* Simpson, U.S. N.M. no. 6177, left lower jaw: a, Crown view; b, external view. Three times natural size.

### PENTACODONTINAE, new subfamily

**Type.**—*Pentacodon* Scott, 1892.

**Distribution.**—Middle Paleocene (and doubtfully Upper Paleocene), North America.

**Diagnosis.**— $P^4_4$  much enlarged.  $P_4$  with very heavy protoconid, sloping backward, well-developed metaconid, and basined heel.  $P^4_4$  with massive, conical, paracone, smaller but sharply distinct metacone,

styles small or lacking, and large, low protocone with widely expanded anterior and posterior cingula.

*Remarks.*—Aside from its probable relationship to the Pantolestinae, this group shows some resemblance to the Anisonchinae and to the Apheliscidae, but in neither case is this resemblance close enough to suggest real affinity. The enlargement of  $P_4$  and the general but primitive stamp of the molars is not unlike the Anisonchinae but does not include any detail such as might indicate a real relationship.  $P_4$  still more resemble those of *Apheliscus* but differ in cusp structure, and the molars are widely different. It is not impossible that *Apheliscus* is an offshoot of the same stock, but real evidence for such a hypothesis is lacking.

#### Genus APHRONORUS Simpson

*Aphronorus* SIMPSON, 1935d, p. 230.

*Type.*—*Aphronorus fraudator* Simpson.

*Distribution.*—Middle Paleocene, Fort Union, Montana.

*Diagnosis.*—Generally similar to *Pentacodon*.  $P_4$  with anterior end less produced downward than in *Pentacodon*, talonid more distinctly basined, with second cuspule more distinct.  $M_{2-3}$  less reduced relatively to  $M_1$ . Trigonids of  $M_{1-2}$  relatively shorter and entoconids relatively higher than in *Pentacodon*. Three talonid cusps of  $M_3$  more distinct.  $P_4$  with metacone well differentiated, protoconule distinct.  $M^1$  and to less degree  $M^2$  slenderer and more transverse than in *Pentacodon*, more leptictid in aspect.

*Remarks.*—This genus is evidently closely allied to *Pentacodon*, and its distinctive characters, taken together, do not definitely suggest that it is necessarily either an earlier or a later stage in the *Pentacodon* phylum. Evolution could have proceeded in either direction, or the two may have diverged from a common ancestry. Nevertheless *Aphronorus* does seem to resemble *Palaeosinopa* in more details than does *Pentacodon* and to this extent may be supposed to retain more of of the primitive characters of the family as a whole, despite its possible divergence in other respects.

#### APHRONORUS FRAUDATOR Simpson

##### FIGURES 22-24

*Aphronorus fraudator* SIMPSON, 1935d, p. 230.

*Type.*—U.S.N.M. no. 6177, left lower jaw with  $P_4$ - $M_3$ . Collected by A. C. Silberling.

*Horizon and locality.*—Gidley and Silberling Quarries, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—Sole known species of genus. Dimensions given in table 27.

*Remarks.*—The lower canine, known from its alveolus only, is large and semiprocumbent.  $P_1$  is very small and appears to have a single



root.  $P_2$  is likewise small but more elongate and with two roots. The only specimen that shows  $P_{1-2}$  is senile and these teeth are truncated by wear at the bases of the crowns.  $P_3$  is larger than  $P_2$  but also small in relation to the whole dentition. When unworn it has a triangular protoconid followed by a heel with a slight internal basin and two rudimentary posterior cusps.  $P_4$  is much enlarged and has a massive protoconid, which slopes backward, and a lower distinct metaconid, closely applied to the posterointernal base of the protocoonid.

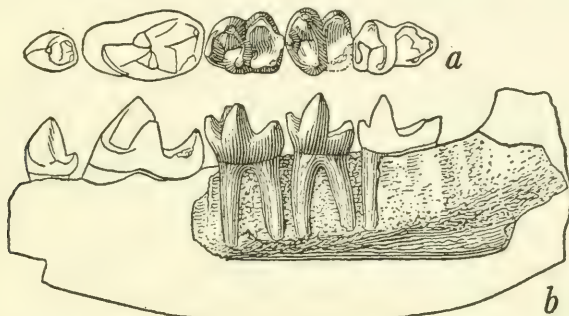


FIGURE 23.—*Aphronorus fraudator* Simpson, U.S.N.M. no. 9448, with parts in outline added from U.S.N.M. nos. 9291 and 9519, right lower jaw: a, Crown view; b, internal view. Four times natural size.

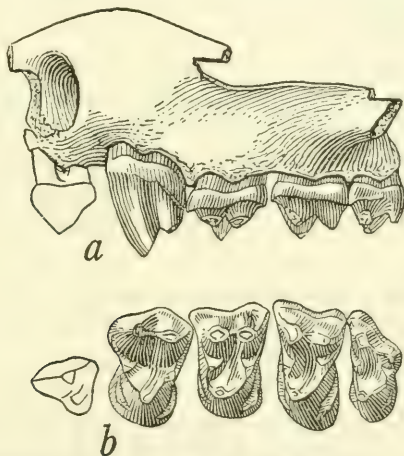


FIGURE 24.—*Aphronorus fraudator* Simpson, U.S.N.M. no. 9560, with tooth in outline added from U.S.N.M. no. 9565, left upper jaw: a, External view; b, crown view. Four times natural size.

nid. Anterior to this there is a sharp internal cingulum, turning into a vertical crest at the anterior midline of the tooth, but there is usually no paraconid or anterior cuspule, although in one or two specimens there is a slight tendency to develop a cuspule here. The large heel has its main cusp external to the midline, connected by a sharp crest to the middle of the trigonid base. Internal to this crest is a basin, and a second, smaller and less distinct cusp is near the posterointernal corner of the tooth.

The lower molars decrease in size from  $M_1$  to  $M_3$ . The paraconids are small and tend to assume a conical shape but are still connected to the anterior protoconid crest. The paraconids are slightly internal to the midline. Metaconids and protoconids are nearly equal. The talonid is wider than the trigonid on  $M_1$ , about equal on  $M_2$ , and narrower on  $M_3$ . On  $M_{1-3}$  the three talonid cusps are about equal in height but the hypoconulid is smallest. On  $M_3$  the hypoconulid is enlarged and projects posteriorly in the usual manner.

The mandible is lighter than in *Pentacodon* and very closely approaches *Palaeosinopa* in all respects.

$P^3$  is 3-rooted and has a single outer cusp like that of  $P^4$  on a smaller scale save for the absence of a metacone. The protocone is small, and there are no cingula.  $P^4$  is a peculiar, large, heavy tooth. Its contour is hourglass-shaped, with median constriction and expanded equal inner and outer lobes. The paracone is nearly circular in section and is heavy and tall and slopes slightly backward, like the protoconid of  $P_4$ . It is followed by a smaller metacone. There is only the vaguest rudiment of a parastyle, but a very small metastyle is present. The protocone is crescentic and large but lower than the paracone. There is a small protoconule and rudimentary metaconule. Approximately equal and expanded anterior and posterior cingula occur on the protocone base, and each tends to develop into a cuspule (protostyle and hypocone). The upper molars are of leptictid type, strongly transverse, with emarginate external shelves, projecting parastylar and metastylar lobes (especially on  $M^2$ ), metacones slightly smaller than paracones, conules distinct, anterointernal cingula, and low hypocones slightly more internal than the protocones.  $M^3$  is reduced in the usual manner, with metastyle and hypocone absent and metacone small.

TABLE 27.—Numerical data on *Aphronorus fraudator*

| Variate               | N  | R         | M           | $\sigma$      | V         |
|-----------------------|----|-----------|-------------|---------------|-----------|
| LP <sub>4</sub> ----- | 10 | 3. 2-3. 8 | 3. 52±0. 05 | 0. 17 ±0. 04  | 4. 9±1. 1 |
| WP <sub>4</sub> ----- | 10 | 2. 0-2. 4 | 2. 15±0. 05 | 0. 14 ±0. 03  | 6. 7±1. 5 |
| LM <sub>1</sub> ----- | 10 | 2. 8-3. 1 | 2. 88±0. 03 | 0. 098±0. 022 | 3. 4±0. 8 |
| WM <sub>1</sub> ----- | 10 | 1. 8-2. 4 | 2. 18±0. 05 | 0. 17 ±0. 04  | 7. 6±1. 7 |
| LM <sub>2</sub> ----- | 12 | 2. 5-2. 9 | 2. 67±0. 04 | 0. 13 ±0. 03  | 4. 7±1. 0 |
| WM <sub>2</sub> ----- | 11 | 1. 9-2. 4 | 2. 17±0. 03 | 0. 114±0. 024 | 5. 2±1. 1 |
| LM <sub>3</sub> ----- | 7  | 2. 6-2. 9 | 2. 79±0. 04 | 0. 10 ±0. 03  | 3. 5±0. 9 |
| WM <sub>3</sub> ----- | 7  | 1. 7-2. 1 | 1. 90±0. 05 | 0. 12 ±0. 03  | 6. 3±1. 7 |
| LP <sub>4</sub> ----- | 8  | 2. 5-3. 1 | 2. 84±0. 06 | 0. 18 ±0. 05  | 6. 3±1. 6 |
| WP <sub>4</sub> ----- | 8  | 3. 5-4. 3 | 3. 88±0. 08 | 0. 22 ±0. 05  | 5. 6±1. 4 |
| LM <sub>1</sub> ----- | 8  | 2. 5-2. 8 | 2. 68±0. 03 | 0. 097±0. 024 | 3. 6±0. 9 |
| WM <sub>1</sub> ----- | 7  | 3. 6-3. 9 | 3. 80±0. 04 | 0. 11 ±0. 03  | 2. 8±0. 8 |
| LM <sub>2</sub> ----- | 4  | 2. 2-2. 6 | 2. 43       |               |           |
| WM <sub>2</sub> ----- | 3  | 3. 9-4. 1 | 4. 00       |               |           |
| LM <sub>3</sub> ----- | 2  | 1. 5-1. 9 | 1. 70       |               |           |
| WM <sub>3</sub> ----- | 2  | 3. 3-3. 6 | 3. 45       |               |           |

## Family MIXODECTIDAE Cope, 1883

Previous views as to the affinities of this peculiar group have been summed up by Matthew (1909, 1915, and Pale. Mem.). In briefer résumé, Cope considered the mixodectids as primates. Matthew (1897) concurred formally but suggested that *Mixodectes* itself might rather be a rodent. Osborn (1902) accepted and expanded this view, defining for the mixodectids a rodent suborder Proglires. Wortman (1903) argued for their return to the Primates. Finally, Matthew (1909 and subsequently) concluded that they probably belong in the Insectivora.

Two very distinctive genera, *Eudaemonema* and *Elpidophorus*, have recently been added to the family. They add to the known variety and have an interesting bearing on relationships within the family, as brought out below, but they do not much alter the evidence for ordinal relationships.

Skeletal remains referred to *Indrodon* by Osborn and Earle and to *Microsyops* by Wortman, in each case considered as indicating primate affinities, have been shown (Matthew, 1909) to be doubtfully or not associated. An astragalus and other fragments referred to *Mixodectes* were at first said by Matthew (1897) to be rodentlike and later (1909) to be equally insectivorelike and in any case not similar to any known primate.

The dentition is said, even by Matthew in rejecting primate affinities, to be primatelike. There is, indeed, some resemblance to various primate genera in a few details, for instance the upper molars suggest *Shoshonius* in general proportions and in the strong mesostyle, and the enlargement of one anterior tooth and development of a diastema by loss of other teeth are also seen in *Tetorius* and some other genera. Such resemblances seem to have no value in the determination of affinities, since they refer to single characters of various different primates that are, in just these characters, highly aberrant among the primates as whole. Aside from such points, which can almost be discarded categorically as more likely to be convergent than not, I detect no primate resemblances in the teeth that go beyond the general Paleocene tuberculosectional pattern common to many different orders at this time. As set forth in the section of this paper dealing with the Primates, the Paleocene and Eocene primates, despite their primitive character, do have a distinctive stamp in molar pattern that is common to all of them and that is not seen to occur in any other order. The mixodectids do not have any of these truly distinctive and (at this time) ordinal primate characters. On the contrary, their high sharp cusps (notably in the talonids), elevated trigonids and internal lower cusps, displaced hypoconulids, and many other distinctive details are quite unknown among any primates and some of



their family characters, such as the ectoloph construction, are approached only as decidedly aberrant *generic* characters by one or a few primate genera.

If we grant Matthew's second opinion that the astragalus of *Mixodectes* does not have diagnostic ordinal rodent characters, the evidence for rodent relationships is little more than the presence of enlarged incisors and (in some but not all genera) of more or less molariform premolars. Both these characters also appear independently in insectivores, numerous different lines of ungulates, primates, marsupials, and other orders. Nor are they really rodentlike in precise detail in this group. Indeed, there now seems to be no actual evidence that the mixodectids are related to rodents.

Granting the usage of Insectivora not only to include the recent groups but also numerous extinct forms that necessitate definition on primitive characters only, we may well call the mixodectids insectivores. Negatively, it may be said that no other defined order could receive them, and positively that their dentition is insectivorelike at least in habitus, that the astragalus is more like that distinctive of insectivores than like any other group except rodents (which are excluded by the dentition), and that in general they have the primitive features by which the Insectivora *sensu lato* are defined.

It is probable that the mixodectids include a related group of phyla that diverged from the primitive placental stock, and apparently from the Insectivora in a more limited sense, at a very early date. Had such a sideline evolved more rapidly, or had it run a longer span and occupied a more important place in mammalian history, it would be more conveniently defined as an order, as, for instance, are the tillo-donts, which probably had a very similar history but developed more striking specializations. Since, in fact, the mixodectids were a short-lived and relatively unimportant group, it is most convenient simply to classify them in the order Insectivora, from which they probably arose.

Within the Mixodectidae there have been included two apparently distinct groups: *Mixodectes* and *Indrodon* of the Torrejon, on one hand, and *Cynodontomys* and *Microsyops* of the Lower and Middle Eocene, on the other. The Torrejon forms are certainly closely related, indeed the distinction between them is not clear, and the Eocene genera are also closely allied and rather difficult to distinguish. Matthew (1915c) defined the two groups as subfamilies, Mixodectinae and Microsyopinae, and he repeatedly expressed doubts as to their really being related to each other, rather than merely convergent. In the lower jaw (the upper being uncertainly known in this respect) the "Mixodectinae" retain a canine, and the enlarged tooth is an incisor, while in the "Microsyopinae" there is only the enlarged tooth

anterior to  $P^2$ . The enlarged teeth are thus not rigidly proved to be the same, and with his customary caution Matthew stressed the fact that they might not be homologous. The premolars are different in the two groups, although I believe that the difference has been over-emphasized. In the "Microsyopinae"  $P^4$  are less elevated and more molariform than in the "Mixodectinae." The molars are almost identical in the two groups, except that in the earlier forms there is a distinct and markedly internal hypocone, while in the later the hypocone is anomalously small and is less internal.

The two genera discovered since Matthew's work, especially *Eudaemonema*, alter this situation. *Eudaemonema* has the anterior (lower) dentition less specialized than in *Mixodectes*, and *Elpidophorus* has it either closely similar to *Mixodectes* or slightly less reduced. In both cases there is no reason to believe that the enlarged incisor is not homologous with that of *Mixodectes* and also with that of *Cynodontomys*. In both genera  $P_4$  is submolariform. In *Eudaemonema* it is very similar to that of *Cynodontomys* and *Microsyops*, rather than to the contemporary *Mixodectes*. In *Elpidophorus* it is aberrant in having a strong, projecting paraconid.  $P^4$  is not known in *Eudaemonema*; in *Elpidophorus* it closely resembles that of the Eocene genera. In *Eudaemonema* the upper molars have strong, internal hypocone, comparable to *Mixodectes*, while *Elpidophorus* is more like the Eocene genera in this respect. These genera thus mingle characters of the "Mixodectinae" and the "Microsyopinae", and they make it impossible to maintain a consistent separation between these groups. At the same time they strongly support the reality of a relationship between them.

For one reason or another the known Paleocene genera of this family cannot be considered ancestral to each other or to the Eocene forms. Thus *Eudaemonema* is the most primitive as regards the retention of anterior teeth, but its premolars are more advanced than in *Mixodectes* and *Indrodon*, and its strong, projecting hypocones seem to exclude it from the ancestry of *Elpidophorus* or of *Cynodontomys* and *Microsyops*. *Mixodectes* and *Indrodon* cannot be ancestral to the later forms for the same reason and cannot be structurally ancestral to the contemporary *Eudaemonema* because of their reduced anterior dentition. *Elpidophorus* has aberrant specializations in  $P_4$  and in details of molar structure that seem to exclude it from consideration as the ancestor of the Eocene genera. Evidently four different groups, intimately related but all on different lines of phyletic descent, are represented. These can be contrasted, among other details, by the characters listed in table 28.

TABLE 28.—*Comparison of dentition of six genera of Mixodectidae*

| Genus                                       | Formula      | P <sub>4</sub>                                                                                    | Internal lower molar cusps                                                                    | P <sub>4</sub>                                      | Upper molars                                    |
|---------------------------------------------|--------------|---------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------|-----------------------------------------------------|-------------------------------------------------|
| <i>Mixodectes</i> and <i>Indrodon</i> .     | 1.1.3.3..... | Elevated, paraconid minute, metaconid rudimentary or absent, talonid poorly basined with 2 cusps. | Slightly or not taller than external. Metaconid opposite or slightly posterior to protoconid. | Elevated, external cone simple.                     | With strong hypocones, projecting internally.   |
| <i>Eudaemonema</i> ...                      | 2.1.4.3..... | About as tall as molars, paraconid small, metaconid large, talonid well basined, with 3 cusps.    | About as in <i>Mixodectes</i> .                                                               | (Unknown)....                                       | About as in <i>Mixodectes</i> .                 |
| <i>Elpidophorus</i> ...                     | 1(+?).1.3.3. | With paraconid large and projecting, otherwise comparable to <i>Eudaemonema</i> .                 | More definitely higher than external. Metaconid slightly anterior to protoconid.              | Less elevated, with separate paracone and metacone. | With weak hypocones, not projecting internally. |
| <i>Cynodontomys</i> and <i>Microsyops</i> . | 1.0.3.3..... | Comparable to <i>Eudaemonema</i> .                                                                | About as in <i>Mixodectes</i> .                                                               | Comparable to <i>Elpidophorus</i> .                 | Comparable to <i>Elpidophorus</i> .             |

A possibility worthy of serious consideration is that the Plagiomenidae may be related to the Mixodectidae. They show the following principal characters suggestive of such a relationship:

Molarization of premolars somewhat similar to mixodectids (except *Mixodectes* and *Indrodon*).

Upper molars with feeble hypocone shelf and pronounced and peculiar median transverse valley (as in *Elpidophorus* and to a less degree some other mixodectids), and otherwise generally but more vaguely similar.

Tendency to emphasize external shelf of upper molars and to develop cuspules on it (but see below).

Elevation of internal over external cusps of lower molars (a tendency in all mixodectids, pronounced in *Elpidophorus*).

Lines joining protoconid to metaconid and hypoconid to entoconid parallel and anterointernal-posteroexternal (tendency in mixodectids, pronounced in *Elpidophorus*).

Paraconids, and trigonids generally, similar.

Molar talonids markedly broadened.

These, and a few minor details, produce a general type of dentition common to plagiomenids and mixodectids and not, as far as I know, to any other groups.<sup>55</sup>

<sup>55</sup> This was evidently partially noticed by Matthew (1918, p. 600), for he notes the resemblance to *Plagiomena* of "an undescribed genus from the Paskapoo beds", which was undoubtedly *Elpidophorus*, not then named and not until very recently known to be an aberrant mixodectid.



On the other hand, the following characters show that the relationship cannot be very close, if it exists at all:

Rather than a single mesostyle developed as a fold of the ectoloph, the plagio-menids have two independent median cusps on the outer shelf of the upper molars.

The anterior incisors (in the lower jaw, at least) are not reduced in number and none is markedly enlarged.

The hypoconulid does not have the characteristic mixodectid displacement toward the entoconid.

The cheek teeth are all deeply furrowed and tend to proliferate cuspules.

The inconclusive evidence of possible relationship of the plagio-menids to the Dermoptera has not been significantly altered since Matthew wrote (1918). The chain of evidence thus tending to link the mixodectids with the Dermoptera is so weak at every point as not to merit serious consideration at present.

### Genus EUDAEMONEMA Simpson

*Eudaemonema* SIMPSON, 1935d, p. 231.

*Type*.—*Eudaemonema cuspidata* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Mont.

*Diagnosis*.—Dental formula,  $\frac{2.1.4.3}{2.1.4.3}$ . Median incisor enlarged. Canine larger than lateral incisor or  $P_1$ .  $P_{1-2}$  small, 1-rooted.  $P_4$  submolariform, with small paraconid, large, high metaconid, and basined, tricuspid talonid. Lower molars as in *Mixodectes*, but trigonids more elevated and all six cusps sharper and more distinct. Upper molars with prominent hypocones, projecting strongly internally.

### EUDAEMONEMA CUSPIDATA Simpson

FIGURES 25, 26

*Eudaemonema cuspidata* SIMPSON, 1935d, p. 231.

*Type*.—U.S.N.M. no. 9314, left lower jaw with C,  $P_2$ – $M_3$ , and roots or alveoli of all other teeth. Found by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry (referred specimen from Silberling Quarry), Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus. Dimensions in table 29.

*Remarks*.—Alveoli in the type and roots in another specimen (no. 9317) show clearly that there was an enlarged median incisor with a procumbent, laterally compressed root, flanked by one much smaller lateral incisor. The canine root is oval, implanted nearly vertically, nearly as large as that of the median incisor, and much larger than that of either of the adjacent teeth. The crown is low, with a simple, spatulate, recurved tip.  $P_1$  is not known, but its alveolus in three different specimens suggests that it was constantly present, although absent in all other known members of this family. Its root is single, small, and circular in section.

$P_2$  has a single but larger root. Its crown is simple, with one cusp, convex on the outer face and excavated anterointernally near the tip, followed by a small, mainly internal heel, not forming a definite cusp.  $P_3$  is larger and has two poorly separated roots. The anterointernal excavation is accentuated and tends to pinch off a very rudimentary paraconid, but there is no trace of a metaconid. The heel rises to a single, distinct cusp.  $P_4$  is nearly molariform. The paraconid is small but distinct and is median. The metaconid is nearly as high as the protoconid, with which it is partly confluent. The talonid is well developed, of about the same width as the trigonid, and has a large hypoconid and smaller entoconid and hypoconulid, the latter median.

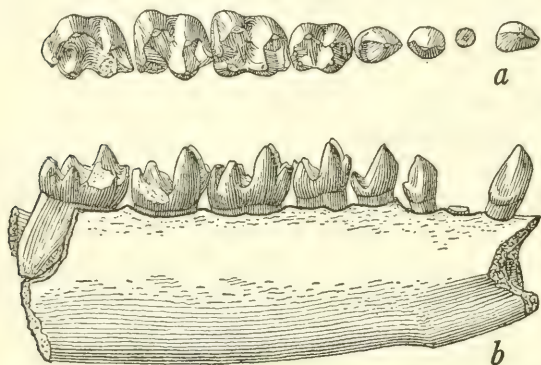


FIGURE 25.—*Eudaemonema cuspidata* Simpson, U.S.N.M. no. 9314, left lower jaw: a, Crown view; b, internal view. Three times natural size.

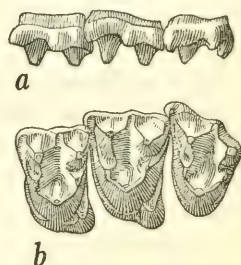


FIGURE 26.—*Eudaemonema cuspidata* Simpson, U.S.N.M. no. 9558, left upper molars: a, External view; b, crown view. Three times natural size.

$M_{1-2}$  are closely similar to each other. The trigonid is moderately elevated and is narrower than the talonid. The paraconid is low and shelflike but is distinct and is united by a crest to the crescentic protoconid. The paraconid is about intermediate between the median and internal positions. The metaconid is slightly higher than the hypoconid, and the hypoconulid is lower and near the entoconid but more distinct from it than in *Elpidophorus*. All three talonid cusps are unusually lofty and distinct. A cuspule tends to develop on the hypoconid-metaconid ridge.  $M_3$  has the talonid narrower, about as wide as the trigonid, and the hypoconulid projects posteriorly and is higher than the other talonid cusps.

Of the four specimens that show the posterior mental foramen, it is beneath  $P_4$  in two (including the type), is double with both under  $P_4$  in another, and in the fourth is beneath  $P_4$  but is followed by another of much smaller size under  $M_1$ . In all cases the anterior mental foramen is larger, pronounced, and beneath  $P_2$ .

U.S.N.M. no. 9558, from the Gidley Quarry, is a left upper jaw with  $M^{1-3}$ . It closely resembles *Mixodectes*, occludes well with some of the lower jaws of *Eudaemonema cuspidata*, and is not what would be expected in the upper jaw of any other known species, so that I place it here with some confidence. Aside from details of proportion, as shown in the figures, the outstanding differences from *Mixodectes* are the better development of the conules, especially the metaconule (almost lacking in *Mixodectes*), and the even greater internal displacement of the hypocone of  $M^2$ .

TABLE 29.—Measurements (in mm) of lower teeth of *Eudaemonema cuspidata*

| U.S.N.M. no. | $P_2$ |       | $P_3$ |       | $P_4$ |       | $M_1$ |       | $M_2$ |       | $M_3$ |       |
|--------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
|              | L     | W     | L     | W     | L     | W     | L     | W     | L     | W     | L     | W     |
| 9314.....    | 1.5   | 1.3   | 2.0   | 1.4   | 2.7   | 1.9   | 3.3   | 2.7   | 3.4   | ----- | 4.0   | 2.6   |
| 9313.....    | ----- | ----- | ----- | ----- | 2.6   | 1.9   | ----- | ----- | 3.5   | 2.7   | ----- | ----- |
| 9317.....    | ----- | ----- | 1.9   | 1.5   | 2.9   | 2.0   | 3.1   | 2.6   | 3.6   | 2.8   | ----- | ----- |
| 9311.....    | ----- | ----- | ----- | ----- | ----- | ----- | ----- | ----- | 3.8   | 2.9   | ----- | ----- |
| 9315.....    | ----- | ----- | 1.9   | 1.6   | 2.7   | 2.2   | 3.0   | 2.7   | 3.4   | 2.9   | ----- | ----- |
| 9316.....    | ----- | ----- | ----- | ----- | 2.7   | 1.9   | 3.2   | 2.7   | 3.5   | 2.9   | ----- | ----- |
| 9670.....    | ----- | ----- | ----- | ----- | ----- | ----- | ----- | ----- | ----- | ----- | 4.1   | 2.4   |

Genus **ELPIDOPHORUS** Simpson, 1927**ELPIDOPHORUS MINOR**, new species

## FIGURE 27

*Type*.—Princeton no. 14201, left lower jaw with  $P_3$ – $M_2$ . Collected by A. C. Silberling.

*Horizon and locality*.—Probably Silberling Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Smaller than *E. elegans* or *E. patratius*.  $P^3$  slenderer than in *E. patratius*, paraconids  $P_4$ – $M_2$  more strictly internal, heel of  $P_4$  smaller and less strongly basined, elevation of inner cusps  $P_4$ – $M_2$  distinct but slightly less pronounced than in *E. patratius*.

*Remarks*.—The type and only known specimen was found by Silberling on January 18, 1903, and is labeled as from the Torrejon, Locality No. 2 (not of the serial list later started and employed in this work). Mr. Silberling states that these data mean the No. 2 beds at or near the Silberling Quarry. It is extraordinary that no further material of this peculiar form seems to occur in the much larger collections made subsequently.

The species is very distinct from the later *E. patratius* of this field, and it will probably prove to be generically different, but they are certainly allied and the present data do not seem to warrant generic definition. *E. minor* resembles *Eudaemonema* more than does *E.*



*patratus*, but it is closer to the latter than to *E. cuspidata* and shows the *Elpidophorus* line to have been distinct at this time.

Dimensions of the type are as follows: Length  $P_3$ , 2.0; width  $P_3$ , 1.4; length  $P_4$ , 2.7; width  $P_4$ , 1.9; length  $M_1$ , 2.8; width  $M_1$ , 2.6; length  $M_2$ , 3.0; width  $M_2$ , 2.8.

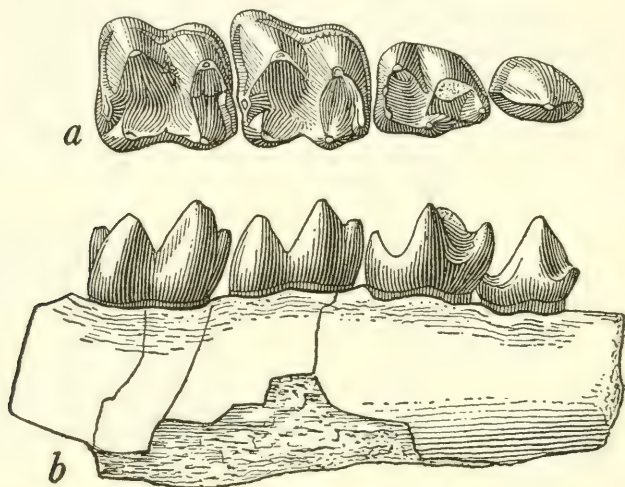


FIGURE 27.—*Elpidophorus minor*, new species, Princeton Univ. no. 14201, left lower jaw: a, Crown view; b, internal view. Six times natural size.

## ?INSECTIVORA, incertae sedis

### PICRODONTIDAE, new family

*Type*.—*Picrodus* Douglass, 1908.

*Distribution*.—Middle and Upper Paleocene, North America.

*Diagnosis*.—Minute insectivorelike or batlike forms of doubtful ordinal affinities, with one pair of greatly enlarged incisors (at least in lower jaw), muzzle long and slender, canines reduced, premolars small with no tendency to molarization, molars large, brachyodont, with shallow, expanded basins and indistinct cusp structure, adaptively resembling molars of the recent Phyllostomatidae.

*Discussion*.—At present only two genera, *Picrodus* and *Zanycteris*, are referred to this family, and these are not directly comparable with each other. The evidence for their close relationship is, however, impelling, as discussed below. The separation of family characters from those merely generic is not entirely practicable in this stage of knowledge, but there can be little doubt that these two genera do belong to a family otherwise unknown, and the characters given in the above diagnosis distinguish them from any other family. The

molars invite comparison with the Phyllostomatidae, although they do not prove that a real relationship exists. The character of the antemolar dentition distinguishes the Picrodontidae sharply not only from the Phyllostomatidae but also from all other Chiroptera.

The affinities of the Picrodontidae are wholly dubious at present. They compare in a very broad and general way with the Insectivora, Chiroptera, and Primates. Reference to the Primates is merely a possibility, with no positive evidence to commend it. Evidence for reference to the Chiroptera is seen in the phyllostomatidlike molars but is really very tenuous and does not at present warrant the extraordinary conclusion that the Chiroptera had already in the Middle Paleocene achieved this peculiar and aberrant molar pattern and at the same time had lost, or not yet acquired, characters otherwise universal among chiropterans. Such references, even when circumspectly expressed, are moreover likely to be misleading, for they inevitably are restated in more general works by authors not acquainted with the original material, in some such form as "Specialized phyllostomatid bats were already present in North America in the Middle Paleocene", without the necessary addition that the evidence actually falls far short of proof. It is more conservative and less prejudicial to future work to refer the Picrodontidae to the ?Insectivora, using Insectivora in its scrap-basket sense, pending discovery of more conclusive indications of affinity. When these are discovered, they are (as far as can be foreseen) as likely to point to the Insectivora as to any other order.

#### Genus PICRODUS Douglass, 1908

*Picrodus* DOUGLASS, 1908, p. 17.

*Megopterna* DOUGLASS, 1908, p. 18.

*Type*.—*Picrodus silberlingi* Douglass.

*Type of Megopterna*.—*Megopterna minuta* Douglass.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Enlarged, procumbent anterior lower tooth, followed by three or four small teeth, the most posterior ( $P_4$ ?) 2-rooted but small and simple.  $M_1$  much enlarged, with a small, elevated, and procumbent trigonid with three poorly differentiated cusps, heel elongate and large, with a curving crest and two vague internal cuspules, basin not closed.  $M_2$  with lower, subquadrate but 3-cusped trigonid, large, oval, basined talonid with crest and two internal cusps. Enamel of both talonids papillated.

*Remarks*.—From Douglass' specimens and, still more, his somewhat diagrammatic figures it would appear altogether impossible that *Picrodus* and *Megopterna* should be synonymous, but this is shown to be true beyond any question by the larger series of specimens now available. The type of *Picrodus* included  $P_4$  and  $M_1$ , the latter imperfect, and that of *Megopterna* included  $M_2$  and a small fragment of

$M_1$  that Douglass mistook for a complete tooth. The type species are synonymous.

Douglass referred *Picrodus* questionably to the Epanorthidae (=Caenolestidae) and *Megopterna* questionably to the Insectivora, without family reference. The resemblance to caenolestids is confined to a vague adaptive similarity to some fossil forms with enlarged  $M_1$  and is not indicative of affinity. *Picrodus* is almost certainly a placental mammal. Among placentals, however, I am not acquainted with any genus with which close and direct comparison is possible. There is, indeed, a vague resemblance to certain highly specialized recent bats, but this does not extend to structural details, is contradicted by the quite different arrangement of the anterior dentition, and is more likely to be misleading than not.

There is one known genus, *Zanycteris*, with which *Picrodus* is almost certainly closely related, although direct comparison is impossible since in *Picrodus* only lower and in *Zanycteris* only upper teeth are known. As I have elsewhere noted (Simpson, 1935a), *Zanycteris* (like *Picrodus*) resembles some recent bats, particularly the phyllostomatids, in adaptive characters of the cheek teeth but is different in details probably of more importance as indices of affinity and in the structure of the anterior dentition, as far as it is known. The great probability of affinity between *Picrodus* and *Zanycteris* is independent of the possibility that they are related to the Chiroptera. In *Zanycteris* the reduction and complete lack of molarization of the premolars, the enlargement of  $M^1$  and reduction of  $M^3$ , and the peculiar papillated coronal enamel are all unusual specializations analogously developed in the lower dentition of *Picrodus*. Furthermore, even in detail the shapes of  $M^{1-2}$  in *Zanycteris* adapt them perfectly for occlusion with lower teeth like those of *Picrodus*. *Zanycteris paleocena* will not occlude with *Picrodus silberlingi*, being a smaller species, but probably a dentition structurally the same as that of *Zanycteris* but of different size would occlude with *Picrodus silberlingi*. *Zanycteris* is known only from one specimen found in the Tiffany, Upper Paleocene, of southwestern Colorado. Its type is certainly not the same species as that of *Picrodus*, and the genera are probably distinct, but not surely. Knowledge of their exact affinities must await discovery of upper teeth of *Picrodus* or lower teeth of *Zanycteris*.

#### PICRODUS SILBERLINGI Douglass

#### FIGURE 28

*Picrodus silberlingi* DOUGLASS, 1908, p. 17.

*Megopterna minuta* DOUGLASS, 1908, p. 18.

*Type*.—Carnegie Mus. no. 1670, right lower jaw with  $P_4-M_1$ . Collected by A. C. Silberling.



*Type of* Megopterna minuta.—Carnegie Mus. no. 1675, left lower jaw with  $M_2$  and part of talonid of  $M_1$ . Collected by A. C. Silberling.

*Horizon and locality.*—Types from Silberling Quarry, most referred specimens from Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—Sole known species of genus. Dimensions given below.

*Remarks.*—From alveoli it is clear that this species had a much enlarged, procumbent anterior tooth, probably an incisor, with a compressed root. U.S.N.M. no. 9866 includes  $M_1$  of *P. silberlingi* and also a loose tooth, which probably is an associated lower incisor. It has a completely enameled crown, curving sharply to a point. The whole crown has a series of eight or nine ridges or angulations, diverging posteriorly from the apex, so that in transverse section it is irregularly polygonal. Aside from these, one side is more convex, the other somewhat excavated, with a slight basal cingulum.

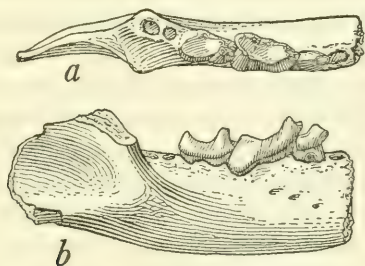


FIGURE 28.—*Picrodus silberlingi* Douglass, U.S.N.M. no. 9622, right lower jaw: a, Crown view; b, external view. Four times natural size.

The anterior tooth is followed by three small, closely spaced, approximately equal alveoli. The material does not indicate whether these were for three separate teeth or for one 1-rooted tooth and one 2-rooted. The next tooth, presumably  $P_4$ , has two roots in the several specimens that show it, not one as stated by Douglass for the type. It has a simple main cusp, more procumbent than shown in Douglass' figure, followed by a small heel. The next tooth, presumably  $M_1$ , is the largest in the jaw and is very peculiar. It differs considerably from Douglass' figure, although I believe that the present specimens do belong to his species and that the discrepancy is due to the worn and broken nature of his specimen and the impossibility of accurate observation except under a binocular microscope at magnifications of 15 or 20  $\times$ . This tooth consists of a trigonid and talonid, but both are greatly modified. The trigonid is small and is produced and procumbent, as if drawn forward and upward in a plastic condition. The protoconid lies near the midline of the tooth as a whole. The metaconid is slightly lower, poorly separated from the protoconid, and internal and slightly posterior to the latter. The

still lower and likewise poorly separated paraconid is almost directly anterior to the protoconid but slightly more internal. The talonid is wider than the trigonid and is very long. It has a crest that begins rather indefinitely on the external side against the base of the trigonid and curves back to the posterointernal corner of the tooth. Its highest part is where it swings internally and across the midline of the tooth, and here it bears two or three vague cuspules. There are also two small cuspules on the inner margin of the talonid, separate from the crest and at a lower level. The more definite of these is just anterior to the posterointernal corner, and the other vague cusp lies between this and the metaconid base. The sloping and volute surface of the talonid, from the crest down to the inner margin, is finely papillated and wrinkled. The lowest point of this surface is at the posterointernal corner, where there is an almost spoutlike exit from the vague talonid basin.

$M_2$  was figured by Douglass ("*Megopterna minuta*"), but his drawing makes the cusps appear more upright, sharp, and distinct than they really are. The trigonid suggests that of  $M_1$  but is much less elevated, the cusps are better separated, the paraconid is more internal, and the trigonid is given a more quadrate form by the angulation of the crest connecting protoconid and paraconid. The talonid is broad and oval, less sloping and more distinctly basined than that of  $M_1$ . The crest defines the posteroexternal angle, instead of curving obliquely across the tooth as on  $M_1$ , and there are two distinct internal cusps, the more posterior of which is connected to the crest. The basin surface is papillated as on  $M_1$ .

$M_3$  is not preserved on any specimen in the collection. From its alveoli, it was smaller than  $M_2$ . Upper teeth have not been recognized.

From the downward curvature of the lower margin posterior to the dental region, it is evident that the angle was of placental type. The mental foramina are numerous and variable. There may be a cluster of three or four in the general region of  $P_4$ . The most constant appear to be a fairly large foramen approximately between  $P_3$  and  $P_4$  and a smaller one about between  $P_4$  and  $M_1$ .

The type is not well preserved, and I have not remeasured it. It may be slightly larger than the other specimens, but there is no doubt that all are conspecific. The most reliably measurable dimension is the oblique maximum diameter of  $M_1$ , that is, a dimension in the midline in a vertical (but not also a horizontal) plane, from paraconid to base of posterior end of talonid.<sup>56</sup> The constants of this dimension in the National Museum sample are: N, 8; R, 2.6–2.9; M,  $2.71 \pm 0.04$ ;  $\sigma$ ,  $0.105 \pm 0.026$ ; V,  $3.9 \pm 1.0$ . The width of this tooth

<sup>56</sup> The ordinary length, a horizontal between transverse, vertical tangential planes, would show great subjective and accidental variation in such a small and peculiarly oblique tooth.

is not so accurately measurable but is recorded within the range 1.0 to 1.3, mean 1.16, for these eight specimens.  $P_4$ , poorly preserved and very difficult to measure, has a maximum oblique diameter of about 1 mm and a width of 0.6 or 0.7 mm.  $M_2$  is well preserved only in the type of *Megopterna minuta*, where it is 1.4 mm in length and about 1 mm in width. The less completely preserved specimens of this tooth do not suggest a deviation of more than 0.1 mm from this.

The one Silberling Quarry specimen in the National Museum collection has  $M_1$  with the dimensions 2.8 and 1.1, well within the range of the Gidley Quarry material.

### Family Uncertain

#### Genus and species undetermined

#### FIGURE 29

U.S.N.M. no. 9777, from the Gidley Quarry, is a right humerus of a fossorial mammal of about the size of a recent *Scalops*. It is imperfect but preserves highly characteristic features. The laterally compressed head, short, stout, twisted shaft, and flattened, widely flaring distal end are disposed in such a way that if the head was directed posteriorly, the entepicondyle was anterior and only very slightly internal in position, and the ectepicondyle similarly posterior, so that the lower arm was thrown outwards almost at right angles to the body. The bicipital groove, mainly occupying the proximo-internal quarter of the posterior face, is deep and narrow, bounded by sharp crests and elevated tuberosities, which are, however, broken off. The pectoralis major insertion is broad and shallow, occupying most of the proximal half of the anterior face of the shaft, and not sharply bounded distally. The deltoid process is broken, but from its base it was more prominent and more internal than in *Scalops*, more proximal and heavier than in *Arctoryctes*. The notch between head and ectepicondyle is nearly semicircular. The distal end has greatly produced epicondyles, the extension of the ectepicondyle far beyond the globular capitulum being especially striking, in comparison with *Scalops*. The other distal articulations are poorly differentiated or preserved. The entepicondylar foramen is strangely developed as a long, small canal, running from the posterior face near the internal margin to the middle of the anterior face of the broad distal end.

This peculiar humerus resembles those of recent moles in many respects but also differs throughout in detail. Unquestionably the resemblance bespeaks similarity of habits. Whether it also indicates phylogenetic affinity is quite uncertain. In some respects resemblance is closer to *Arctoryctes* from the Oligocene (see Schlaikjer, 1933), but there are also numerous differences: The distal end is more nearly parallel to the long (anteroposterior) axis of the head; the deltoid



process is less internal, stouter, and more proximal; the ectepicondyle is more produced; the entepicondylar foramen, or rather canal, is longer; and other differences of proportion and detail are seen. Nevertheless a relationship seems probable. The *Arctoryctes* humerus was supposed by Matthew to belong to a chrysochlorid, but Schlaikjer has shown that the evidence is all against this view and favors talpid affinities. *Arctoryctes* may belong with the dentitions and skulls known as *Proscalops*.

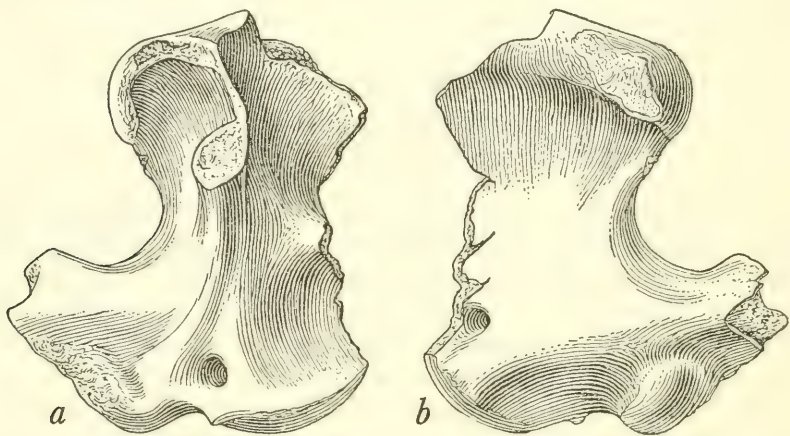


FIGURE 29.—Humerus of an unidentified fossorial mammal: *a*, Anteroexternal face; *b*, posterointernal face. Four times natural size.

On the basis of the teeth, no genus known from the Gidley Quarry would seem to be closely allied to *Proscalops*. Some nyctitheriids have been supposed to be talpids or at least talpoids, but the only probable nyctitheriid in this fauna, *Stilpnodon simplicidens*, is too small to have had this humerus. The humerus does not belong to a multituberculate nor to any other order known in this fauna save the Insectivora. It is not leptictid and cannot belong to *Aphronorus* if that genus is really a pantolestid, but might if the genus does not belong with *Palaeosinopa* and *Pantolestes*. It might belong to *Gelastops* but probably does not if that genus is correctly considered an ally of *Didelphodus*. *Eudaemonema* shows some, but only very distant, resemblance to such dentitions as *Proscalops* and might conceivably have had a fossorial humerus. The dentition of the animal represented by this humerus may be unknown, although this is improbable in view of the many jaws and few humeri collected from the quarry.

In any event the presence of such a specialized fossorial animal in this ancient fauna is of great interest.

## Order PRIMATES Linnaeus, 1758

The Fort Union primates are of exceptional interest as the oldest known members of the order to which man belongs, and any light that they can cast on the early history of this great group is highly important. Dr. Gidley fully recognized these facts, and when the arduous task of preparation was finally completed, he turned first to the primates in beginning his definitive work. His previous papers were all preliminary and provisional, but he completed the primate section of his proposed memoir and published it in 1923 as a separate paper, later to be united with the other proposed sections into a single monograph. No other section was ever finished, and the primate paper was Gidley's last contribution to the Paleocene.<sup>57</sup>

When these primates were discovered they were far the oldest known. Many primates were known from the Eocene of Europe and North America, but only one, *Plesiadapis*, was known from the Paleocene, and this was considered as only very doubtfully primate and is considerably younger than the Fort Union primates of Gidley's collection. After Gidley's discovery, but before its publication, Matthew (1915) added *Nothodectes* (= *Plesiadapis*) also from the Paleocene, and in 1921 Matthew and Granger added several more genera from the Tiffany, but these are all younger than Gidley's material. Jepsen and I have made recent additions to the known upper Paleocene primates, but only *Plesiolestes* Jepsen, 1930, is of an age comparable to Gidley's genera, and there is no reason to suppose that it is older.<sup>58</sup>

It is in accord with Gidley's intention that these forms are here redescribed in connection with the whole fauna, despite their publication previously. This is the more necessary because since Gidley's publication knowledge of early primates has been greatly increased both by discovery and by revision, calling for reconsideration of many points that he mentioned. For this reason, his diagnoses and discussions are not quoted in full, but are revised in the light of the wider knowledge of today and of the somewhat different conclusions to which this has led me.

Gidley recognized four new genera in this fauna and placed six species in them. The fact that two species are based on upper jaws, with lowers referred, and the other four on lower jaws, with uppers referred to three of them, introduces a slight element of doubt, but on the basis of the lower jaws, at least, it is certain that six species are represented and that Gidley's identifications of all these specimens are

<sup>57</sup> With the minor exception of a very brief note on the Tiffany.

<sup>58</sup> Abel (1931) lists *Plesiolestes* as from the Lower Paleocene and suggests that it is the oldest known primate, but it is from the middle Paleocene and not appreciably, or not at all, older than the genera here discussed, one of which it closely resembles.

correct. The only taxonomic change to be introduced is that a fifth genus is made to receive a species that Gidley placed doubtfully in *Palaechthon*.

### Family ?ANAPTOMORPHIDAE Cope, 1883

In this fauna the three genera *Paromomys*, *Palaechthon*, and *Palenochtha* are very tentatively listed with the Anaptomorphidae, although (as will appear) the relationship is not clear and this whole complex of early primates is highly polyphyletic and very confusing.

*Paromomys*, *Palaechthon*, and *Palenochtha* evidently belong to slightly divergent lines, but they have certain characters in common. The most important of these are:

1. An enlarged, semiprocumbent lower incisor, its root not extending beneath  $P_4$ .
2. Other lower incisors vestigial and variable or absent.
3. Lower canine present and only slightly reduced.
4.  $P_1$  and probably sometimes  $P_2$  absent.<sup>59</sup>
5.  $P_4$  little or not enlarged, trigonid simple, elevated, with low, 2-cusped talonid.
6. Molar trigonids with small, generally short and quadrate basins, paraconids generally distinct but reduced, cusps marginal or nearly so.
7. Heels of  $M_{1-2}$  large, simple, broadly basined.
8.  $M_3$  with third lobe, which, however, differs greatly and characteristically in the three genera.
9.  $P^3$  (as far as known) 2-rooted and not transverse.
10.  $P^4$  transverse, strong protocone, paracone and metacone little or not differentiated, conule feeble or absent.
11. Upper molars without mesostyle, protostyle, or hypocone; two small but distinct conules; posterointernal corner of crown expanded and basined to varying degrees; inner face of molar with vertical groove at least on  $M^2$ .

These suggest a possible fairly immediate common origin for the three genera, but they are diverging from each other, principally as follows:

*Paromomys*: Antemolar dentition of unmodified basic type as listed above. Molar trigonids very short and quadrate, paraconid almost disappearing by fusion with metaconid on  $M_{2-3}$ . Third lobe of  $M_3$  very strong, with at least two distinct cusps. Inner base of  $M^2$ , at least, more or less bilobed. Posterointernal expansion of upper molars very marked.

*Palaechthon*:  $P_4$  more progressive, with distinct paraconid and metaconid. Molar trigonids less quadrate and paraconids more distinct. Third lobe of  $M_3$  weaker but still with two cusps. Upper molars not bilobed, posterointernal expansion less.

*Palenochtha*: Anterior dentition further modified by loss of another tooth, probably  $P_2$ .  $P_4$  much as in *Paromomys*.  $M_3$  with weak, 1-cusped third lobe. Upper molars not bilobed, posterointernal expansion slight.

Except for the absence of  $P_2$  (which, however, is not absolutely certain), *Palenochtha* seems definitely the most primitive of the three and its general structure is such as might be expected in the ancestry of

<sup>59</sup> Certain homologies, discussed on a later page, are here assumed. Exact identification is impossible, but as the teeth are probably homologous between the genera in question, if they are labeled consistently it does not matter from the point of view of determining affinities whether the labels prove to be correct or not.



both the other genera. *Paromomys* and *Palaechthon* show crossing specializations. The general molar structure of *Palaechthon* is specialized more or less in the direction of *Paromomys* but is less aberrant, while its  $P_4$  is definitely more progressive. *Paromomys* shows distinctly the most aberrant molar structure but has  $P_4$  still relatively unprogressive.

The only known primate of comparable age is *Plesiolestes* Jepsen, from a Torrejon equivalent in the Fort Union of northern Wyoming. Its age is not appreciably different from that of the Gidley Quarry specimens, and the geographic locality is not very distant, all occurring in the same widespread formation. Jepsen tentatively referred his genus to the Plesiadapidae but noted (1930a, p. 506) that "there are many structures on the two specimens which are not like those of other Plesiadapids." He did not compare with Gidley's previously published genera, which *Plesiolestes* resembles in many ways. The anterior alveoli show an enlarged semiprocumbent incisor and a smaller, less procumbent canine, as in all three of Gidley's genera here discussed, and also a moderate  $P_2$ , as in *Paromomys* and *Palaechthon*.  $P_3$  is also closely similar, but relatively larger, being about as high as  $P_4$ , whereas in Gidley's genera it is lower.  $P_4$  closely resembles that of *Palaechthon*, the only difference clear from the available data being that in *Plesiolestes* the heel is wider and the paraconid and metaconid stronger, especially the latter. The molars are very similar to those of *Palaechthon* and seem to me to show no difference of probably generic value.

While *Plesiolestes* may be provisionally accepted as valid, chiefly on the basis of the more progressive  $P_4$ , it is almost surely very closely related to *Palaechthon*, and the distinction of the genera is not at present wholly satisfactory. If, as is possible, *Plesiolestes* is somewhat younger, it could well be a slightly modified and progressive descendant of *Palaechthon*. Its diagnostic features, as against *Palaechthon*, seem to me modifications away from as much as toward the plesiadapids. In any case it is surely closer to *Palaechthon* than is either genus to any undoubted plesiadapid, and if a plesiadapid relationship exists at all, *Palaechthon* is probably less removed from that line than is *Plesiolestes*.

*Palenochtha*, the least aberrant of the present genera as regards comparison with an abstract protoprimate dentition, seems to resemble the Eocene tarsiods (in the broadest sense) more than any other known mammals. The specialization of the anterior lower teeth is not exactly as in any later tarsiod but is within the apparent potentialities of the group. *Omomys*, from the Bridger,<sup>60</sup> has two enlarged

<sup>60</sup> The American lower Eocene species placed in *Omomys* are very doubtfully congeneric with the Bridger genotype. As noted by Teilhard, the European lower Eocene specimens are very distinctive and might be, in my opinion definitely are, representative of a different genus but one close to and perhaps structurally ancestral to true *Omomys*.

anterior teeth followed by three premolars, but in it there is a small tooth between these two enlarged teeth, which is either much more reduced or wholly absent in the much older Fort Union genera. *Absarokius* may very closely resemble the Fort Union genera in the anterior teeth, although this is very dubious, as they are known in *Absarokius* only from poorly preserved alveoli of one specimen, which seems to show less disparity between the incisor and the ?canine. *Tetonius* and the European *Necrolemur* have a single enlarged anterior tooth,<sup>61</sup> a condition that could be derived from that of the middle Paleocene genera, although there is no adequate evidence that it was so derived.

P<sub>4</sub> is more primitive in *Palenochtha* than in any later tarsioid genus known to me, but the difference in such forms as *Anaptomorphus* or "*Omomys*" *belgicus* is not marked, and as the increasing and diverging specialization is in keeping with the relative ages it has no crucial bearing on general affinities. The lower molars of *Palenochtha* are much like those of ?*Omomys vespertinus*, "*Omomys*" *belgicus*, and similar forms, that is, those Eocene tarsioids in which the molars are least specialized. The same may be said of the upper molars: those of *Palenochtha* show distinctions by which the genus may be recognized (such as the internal groove and more inclined protocone), but they very closely resemble the least aberrant Eocene tarsioids. Comparison with ?*Omomys vespertinus* is especially suggestive of affinity. Most later genera differ in the manifestly progressive development of secondary internal cusps.

It is, incidentally, worthy of note that *Palenochtha* has no known character that would exclude it from ancestry to *Tarsius*, itself, although of course the absence of intermediate stages makes this observation unworthy of being advanced except as an interesting but wholly untested possibility.

The more advanced P<sub>4</sub> of *Palaechthon* does not call for detailed consideration. It is in line with progressive changes in many tarsioids and some other primates, although it should be noted that the development of P<sub>4</sub> in the *Tetonius*, *Carpolestes*, *Apatemys*, *Plesiadapis*, and some other groups lies along distinctly different lines.

The peculiar molar structure suggested in *Palaechthon* and fully developed in *Paromomys* is more distinctive. The short quadrate trigonid and marginal paraconid approximated to the metaconid appear among tarsioids in only one or two later genera. *Absarokius* has very similar trigonids on M<sub>2-3</sub>, but that of M<sub>1</sub> is more elongate, probably secondarily in connection with the shearing development of P<sub>4</sub>. Other American tarsioids are more distinctive. Among European forms, only *Necrolemur* and *Microchoerus* are similar, and they are

<sup>61</sup> Commonly called the canine, but it seems to me more probable that it is an incisor in both cases.

more advanced in the reduction of the paraconid, but are much younger. The broad third lobe of  $M_3$  and double hypoconulid also appear in *Necrolemur* and *Microchoerus*, but not in *Absarokius*. Among American tarsiods only *Washakius* has a similar talonid on  $M_3$ , and its trigonids are quite different.

The characteristic posterointernal upper molar expansion and basining of *Paromomys* are suggested in many later tarsiods, such as *Absarokius*, *Hemiacodon*, *Shoshonius*, *Tetonius*, and, in Europe, *Nannopithec* (most marked in *Absarokius* and *Nannopithec*), but in all these the structure is much less marked. In some cases (e. g., *Tetonius*) it is so slight that it is noted only by special search with *Paromomys* in mind, and in all the instances mentioned there is the characteristic distinction that a posterior cingulum passes internally beyond the limits of the incipient (or vestigial) basin and tends to form a hypocone at its inner end. This could be a specialization from the *Paromomys* condition, but the difference is clear and there is no evidence of certainly intermediate stages. In the European *Necrolemur* (and its highly modified ally, *Microchoerus*), however, the hypocone is on the rim of a basin much like that of *Paromomys*, and structural ancestry as regards this character is quite possible but hypothetical.

In summary comparison with the acknowledged tarsiods, there are resemblances throughout and every separate structure of the Fort Union genera is approached in some later genus. The fundamental similarity is most clear in *Palenochtha*, but even in this most generalized type the anterior dentition is too specialized for ancestral relationship to any known later genera but *Tetonius*, *Necrolemur*, *Microchoerus*, and (still more doubtfully) *Absarokius*, and in these cases the minor morphological differences are also marked and annectant forms unknown. *Paromomys* and *Palaechthon* also resemble various later genera, but in most cases crossing specializations make any approach to direct phyletic connection impossible. *Absarokius* is, on the whole, the most similar American form, but in several respects it is apparently less specialized; for instance, in the simpler heel of  $M_3$ , probably less enlarged incisor, and smaller protocone of  $P^4$  (which may, however, be secondary), despite its younger age.

The European genus *Necrolemur*<sup>62</sup> compares more closely with *Paromomys* than does any known tarsiod to the extent that it exhibits all the principal specialized characters of *Paromomys* and that while it has numerous additional specialization of its own, no crossing specialization is involved. Its dental formula is probably  $\frac{2.1.3.3}{1.1.3.3}$ . Stehlin (1916) has placed this upper formula beyond any serious question. He gives the lower formula as  $\frac{0.1.4.3}{0.1.4.3}$ , but the evidence is very unconvincing. *A priori* it is highly improbable that an enlarged median

<sup>62</sup> The following remarks apply equally to *Microchoerus*, except that the latter is much more highly specialized in the dentition. If *Necrolemur* comes from *Paromomys*, then, *ipso facto*, *Microchoerus* does also but has evolved more rapidly.



tooth should be a canine, that  $P_1$  should be present in an upper Eocene tarsiod when it is absent, as far as surely known, in every other known tarsiod even in the Paleocene, or that an enlarged lower canine should occlude against an enlarged first upper incisor and anterior to a second upper incisor. The occlusion in itself is so suggestive of an incisor that only the strongest contrary evidence would warrant any other conclusion, and the other considerations seem to place this almost beyond doubt. It is true that in *Tarsius* the largest anterior mandibular tooth is the canine, but as Stehlin (1916) himself has shown the analogy with *Necrolemur* is very distant, and in *Tarsius* the lower canine occludes between  $I^2$  and C as would be expected, not between  $I^1$  and  $I^2$ . Furthermore, the actual formula in *Tarsius* is  $\overline{1.1.3.3}$ , as I believe it was also in *Necrolemur*.<sup>63</sup>

If this formula be accepted for *Necrolemur*, its anterior dentition could be derived from that of *Paromomys* by further enlargement of the already enlarged incisor and great reduction of the canine, still of moderate size but not enlarged in *Paromomys*. The premolars of *Necrolemur* are broader, lower, and more proclivous than in *Paromomys*, and there is a distinct metaconid on  $P_4$ . The lower molar structure is closely similar throughout except for details in *Necrolemur* like the complete loss of separate paraconid on  $M_{2.3}$ , which are the logical continuation of tendencies clearly present in *Paromomys*.

In the upper jaw, the 3-rooted  $P^3$  of *Necrolemur* is also progressive.  $P^4$  and the molars are less transverse than in *Paromomys*, a feature of no clear significance. The protocone of  $P^4$  may be smaller in the later genus; if so, it is the only character that suggests, and it does not prove, that *Necrolemur* could not be derived from *Paromomys*. Aside from their proportions, the upper molars of *Necrolemur* differ in having stronger conules (the metaconule double) and distinct hypocones, but the basic plan is remarkably similar, as already suggested.

As far as the dentition goes, it must be concluded that *Necrolemur* and *Paromomys* are probably rather closely related, and the latter could be ancestral to the former. The conclusion is obviously unproved and open to doubt. Corresponding with their great separation in space and in time, the genera do differ markedly and annectant types are unknown, but the fundamental similarity is striking.

*Trogolemur*, *Uintalestes*, and *Phenacolemur* are all *incertae sedis*, but all show some special resemblances to *Paromomys* and its Fort Union allies. *Trogolemur* has the same dental formula as *Paromomys*,  $\overline{1.1.2.3}$ . The incisor is relatively larger, and the next tooth, presumably the canine, is very small. The premolars are more expanded

<sup>63</sup> Although the case is less clear, by analogy it seems probable that the enlarged median mandibular teeth of *Tetoniuss* are also a pair of incisors, not canines as generally supposed following Matthew. I should write the *Tetoniuss* formula either  $\overline{1.0.3.3}$  or  $\overline{1.1.2.3}$ , of which the second is perhaps slightly more probable. (Matthew wrote  $\overline{0.1.2.3}$  but this is an evident lapsus, and he clearly meant to write  $\overline{0.1.3.3}$ .)

transversely but otherwise similar.  $P_4$  has a metaconid.  $M_{1,2}$  are much like *Paromomys*. The third lobe on  $M_3$  is narrower than in *P. maurus* but closely approached in *P. depressidens*. The cheek teeth throughout are very close to *Palaechthon* but lower, broader, and heavier. *Palaechthon* is an admirable structural ancestor for *Trogolemur*, although the time gap is too great for definite decision.

*Uintalestes* is very poorly known but is evidently related to *Trogolemur* from which it differs essentially only in the further dental reduction, having only seven teeth in the lower jaw, and the narrower heel of  $P_4$ .

The lower molars of *Phenacolemur* could readily be derived from the *Paromomys* type but are heavier and more quadrate.  $P_4$  is also similar but is much enlarged and likewise heavier and more quadrate. The much heavier incisor and the complete loss of all teeth between it and  $P_4$  sharply distinguish *Phenacolemur*, however, and the time gap is far too short for derivation from *Paromomys*. The molar resemblance may, therefore, be misleading.  $P^4$  has a much stronger posteroexternal cusp than in *Paromomys*, and the internal groove is absent on the upper molars, but they have an equally and similarly expanded posterointernal basin and in general are as close to those of *Paromomys* as are the lower molars.

Resemblances to the *Carpolestes* and the *Plesiadapis* phyla are discussed in dealing with the contemporary members of the latter, *Elphidotarsius* and *Pronothodectes*, but the adaptively related group Apatemyidae has no known representative before the upper Paleocene. They may, however, be summarily dismissed as possible close relatives of the Fort Union forms, as none of their peculiar distinctions are foreshadowed in the latter. The apatemyids, as redefined by Jepsen (1934), have an enlarged incisor, larger than in *Carpolestes* or *Plesiadapis*, which more nearly resemble *Paromomys* and its allies in this respect, and early lose all teeth between this and  $P_3$ , at least two of which are retained in *Paromomys* and in the other two groups mentioned.  $P_3$  becomes 1-rooted and peculiarly bladed.  $P_4$  is markedly reduced even in the upper Paleocene and becomes vestigial in later forms. The molars have a quadrate trigonid, as in many early primates, but, especially on  $M_1$ , it is much more elongate anteroposteriorly than in *Paromomys* and its allies. The upper teeth are equally divergent.

Gidley (1923, pp. 3-4, 8-9) noted the resemblance of *Paromomys* and *Palaechthon* to the Notharctinae in the lengthened heel of  $M_3$ , the trigonids consisting chiefly of protoconid and metaconid connected by a loph and with an anterior shelf, and the posterointernal expansion and basining of the upper molars. He added, however, that these are not exclusively notharctine characters and concluded that they did not indicate close affinity in this case. The resemblance is,

indeed, very close, and as far as the posterior teeth are concerned the differences involve only a few minor details of apparent generic or lesser value. The anterior teeth, however, are very different and are much more specialized in the earlier genus. *Pelycodus* has the formula  $\frac{2.1.4.3}{1.1.3.3}$  as against  $\frac{1.1.3.3}{1.1.3.3}$  in *Paromomys* and *Palaechthon*, its incisors are small and its canine large. Furthermore, the *Paromomys*-like molar characters of *Pelycodus* are not seen in *Adapis*, but the Nothartinae, to which *Pelycodus* belongs, and the Adapinae show a fundamental resemblance in skull and skeletal structure, which leads (Gregory, 1920, and elsewhere) to their association in one family. And this general structure is very unlike that of the supposedly tarsiid genera, such as *Tetonius* or *Neurolemur*, with which there is equal or greater reason for supposing *Paromomys* to be related.

To propose as a tentative solution of this extraordinarily intricate problem that *Paromomys* is a derivative of a tarsiid-nothartine ancestry is not fully satisfactory, for a corollary would be that the Nothartinae were descended from a different tarsiid or protarsiid ancestry from the Adapinae, one with more *Paromomys*-like molars, and this is wholly unsatisfactory on the basis of the mutual relations of Nothartinae and Adapinae as inferred from their own much better known structures. It is much more probable either that the marked resemblance in the molars of *Paromomys* and *Pelycodus* is wholly convergent or that *Paromomys* is really a divergent offshoot of the earliest nothartine ancestry toward which various tarsiids have converged in one way or another. The second alternative would imply extreme antiquity of the *Pelycodus* pattern and the very remote separation of Nothartinae and Adapinae, to a degree that seems improbable. The very tarsiid, and not particularly *Pelycodus*-like, pattern of *Palenochtha*, which nevertheless seems almost surely to be a fairly close relative of *Paromomys* and *Palaechthon*, and the many distinctly tarsiid characters of the latter genera, however eclectic in their combination, also suggest that the former alternative is more probable, as Gidley concluded. I must confess, however, that I see no way of forming a really strong and reasonable opinion on this problem from the present evidence.

#### Genus *PAROMOMYS* Gidley

*Paromomys* GIDLEY, 1923, p. 3.

*Type*.—*P. maturus* Gidley, 1923.

*Distribution*.—Middle Paleocene, Fort Union, Mont.

*Diagnosis*.—Dental formula probably  $\frac{2.1.3.3}{1.1.3.3}$ . Lower incisor enlarged, root extending beneath  $P_2$ . Canine normal or slightly reduced.  $P_2$  present, 2-rooted.  $P_4$  not enlarged, paraconid and metaconid very rudimentary or absent, trigonid apex slightly higher than  $M_1$ , heel low, bicuspid. Molars with short trigonids, with closed, small,



quadrangular, transverse trigonid basins, paraconids small and closely approximated to metaconids, especially on  $M_{2-3}$ ; cusps. submarginal; no metastylid. Talonid of  $M_3$  greatly enlarged, with strong third lobe with (at least) two distinct, transversely paired cusps.  $P^3$  2-rooted.  $P^4$  3-rooted, with strong protocone, no distinct metacone. Upper molars primitively tritubercular, without mesostyle, protostyle, or hypocone, but with a ridge from the protocone swinging around the posterointernal corner, which is much expanded and basined. Internal bases generally bilobed.

The morphology of the genus is described under its type species, and the distinctive characters of the second species mentioned under it.

#### PAROMOMYS MATURUS Gidley

FIGURES 30, 31; PLATE 7, FIGURES 2, 2a, 3, 3a; PLATE 8, FIGURES 2, 2a, 3, 3a  
*Paromomys maturus* GIDLEY, 1923, p. 3.

*Type*.—U.S.N.M. no. 9473, right lower jaw with  $P_4$ – $M_3$  and anterior alveoli. Collected by A. C. Silberling.

*Horizon and locality*.—All known specimens from *Gidley Quarry*, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Trigonids  $M_{1-2}$  notably narrower than talonids.  $P^4$  strongly transverse. Internal bases of  $M^{1-2}$  strongly bilobed. Measurements and derived statistical data given below. Dental formula  $\frac{7.1.3.3}{1.1.3.3}$  (but see below). All teeth closely placed, without diastema.

*Discussion*.—There are six specimens in which the anterior alveoli are all shown, although in none are their rims unbroken. One of these, as noted by *Gidley* (1923, p. 9—*Gidley* mentions two, but the other is not of this species), has a minute pit external to and between the incisor and canine, which might be an alveolus for a vestigial incisor. It could, however, be a mere break, and as none of the other five specimens shows it this is a more probable explanation.  $I_2$  was thus probably absent, and if ever present was vestigial and oftener lacking.

The incisor and canine are unknown except by their alveoli. The incisor was large, its root slightly compressed laterally, and was semi-procumbent, its root extending to beneath the posterior end of  $P_2$  or anterior end of  $P_3$ . The canine was considerably smaller, its nearly circular root with about half the (maximum) diameter of  $I_1$ . It is less procumbent, and its root is shorter than that of  $I_1$ , the root of which passes beneath it. The one canine root occupies about the same space as the two of  $P_2$ .

$P_2$  has two separated, divergent roots. The crown is high, slender, very slightly procumbent, and somewhat recurved at the tip. The outer face is convex, the inner excavated anteriorly and posteriorly, adjacent to curving, vertical sharp anterointernal and posteroexternal crests.

On one specimen (9479) there is a very minute anterior cuspsule, high on the crown, which is only very vaguely suggested on a second specimen surely of the same species (9676). There is a low and very small heel, with a minute cusp at the posteroexternal corner of the

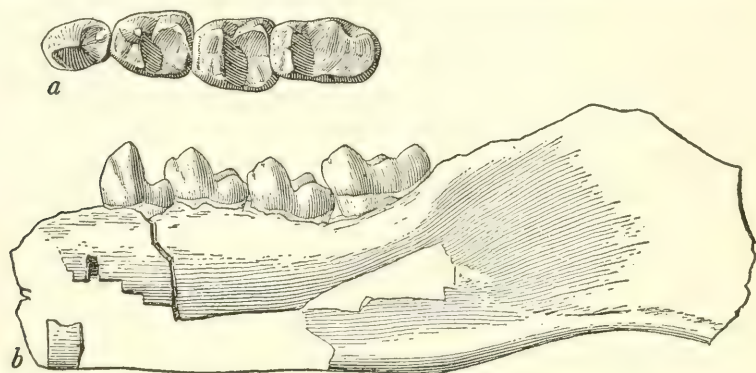


FIGURE 30.—*Paromomys matusus* Gidley, U.S.N.M. no. 9473, right lower jaw: *a*, Crown view; *b*, internal view. Four times natural size. (After Gidley, 1923, fig. 1.)

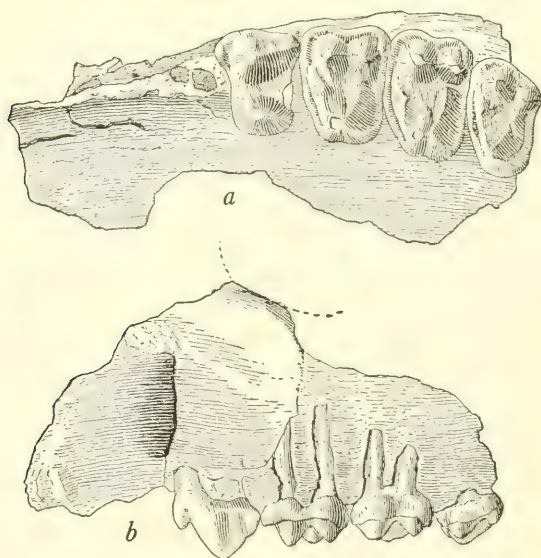


FIGURE 31.—*Paromomys matusus* Gidley, U.S.N.M. no. 9540, left upper jaw: *a*, Crown view; *b*, external view. Four times natural size. (After Gidley, 1923, fig. 2.)

tooth, at the base of the posterior crest, from which a ridge passes downward and internally to the posterointernal corner.

$P_3$  has about the same length and height as  $P_2$  but is considerably wider and more robust. The anterior crest is median near the apex and turns inward below this, an accentuation of the slighter curve of

this crest on  $P_2$ . The posterior crest is less curved and is only slightly external to the midline, the tooth being much more swollen external to it than is  $P_2$ . The heel is more definite, much wider, the cusp less external, and the ridge less sloping.

$P_4$  is much longer and wider and somewhat higher than  $P_2$ , shorter, slightly narrower and somewhat higher than  $M_1$ . Aside from its greater size, it differs from  $P_3$  chiefly in the much stronger heel. A small cusp appears at the posterointernal angle, and a ridge running anteriorly from this tends to close a small basin. A minute cuspule may appear about halfway up the crown on the inside of the anterior edge, but this rudiment is often lacking even on unworn teeth. Similarly, a very vague rudiment of a metaconid appears on the most progressive variants (e. g., 9545) but is oftener absent.

The molars have small trigonids and large basined heels. On  $M_1$  the trigonid is well elevated and is directed somewhat forward, while on  $M_{2-3}$  it is progressively lower. On  $M_{1-2}$  the talonid is considerably wider than the trigonid, the inner face of the tooth base being along a straight anteroposterior line and the outer face strongly oblique. On  $M_3$  the trigonid and anterior half of the talonid are of about equal width. The enamel is nearly smooth, but on completely unworn teeth the basin is somewhat wrinkled. Variable, crenulated external cingula are developed on all the molars except on the third lobe of  $M_3$ . There are no internal cingula.

The paraconid is present on all the molars and is anterior and slightly external to the metaconid. On  $M_1$  it is definite and well separated from the metaconid, although small. On  $M_{2-3}$  it is much closer to the metaconid and is almost fused with the latter, disappearing with slight wear. On  $M_1$  the metaconid is about equal to the protoconid, and on  $M_{2-3}$  it is higher. On all, the metaconid is internal and slightly posterior to the protoconid, and the two are connected by a notched crest. Another, less prominent crest runs forward and slightly inward from the tip of the protoconid to the anteroexternal angle of the tooth, then internally along the anterior rim to the paraconid, enclosing a short, transverse, very shallow and small trigonid basin.

$M_{1-2}$  have typical hypoconid and entoconid of about equal height. The sharp basin rim is vaguely expanded in the hypoconulid region, but no definite apex is here formed. There are no metastylids.

The heel of  $M_3$  is very elongate, with two definite lobes each primarily with two large cusps, one external and one internal. The posterior, or hypoconulid, lobe may be further complicated by the incipient fission of one or both of its cusps, and adventitious cuspules may even appear in the basin, the exact structure of this part being highly variable, although its basic features, the extension of the basin into a third lobe and the strongly double hypoconulid, are constant.



The symphysis is short, unfused, and relatively deep. There is a larger mental foramen beneath  $P_2$  or the posterior part of the canine and another, smaller, beneath  $P_4$ . The dental foramen was far back of the molars and slightly below the alveolar level. The angular process is not completely preserved in any case but was directed decidedly downward, as well as backward, and evidently was strong and more or less styliform. Condyle and coronoid are not preserved.

The upper canine is represented only by part of its alveolus in one specimen (9540). This suggests that it was strongly reduced, the portion of alveolus preserved indicating a root not larger than the posterior root of  $P^2$ .  $P^{2-3}$  are known only from alveoli. Each had a small anterior and large posterior root. On  $P^3$  the disparity is greater, and the posterior root more transverse, but even it apparently does not have a third root, and the inner heel, or protocone, must have been small.

$P^4$  is a large, transverse tooth with three separate roots. The high outer cusp, paracone or amphicone, is vaguely triangular and is single, only very slight inner and outer vertical depressions suggesting the incipient appearance of a metacone on its posterior slope. There is a small, distinct parastyle and a much less distinct metastyle higher on the crown than the parastyle. The posterior half of the outer face has a narrow, sharp basal cingulum. The protocone is large and definite but lower than the amphicone, and its apex is anterior to a median transverse line across the tooth. From it a small sharp, cingular crest runs to the parastyle. Another crest falls away directly posteriorly from its apex to the expanded posterointernal angle of the crown, where it turns nearly at right angles and becomes a well-developed but simple posterior cingulum. A minute, isolated cuspile appears in the position of a metaconule.

$M^1$  and  $M^2$  are almost identical in structure, differing only in outline and proportions. Paracone and metacone are strong, distinct, and nearly equal, the paracone very slightly larger. There is a strong external cingulum, rising at the anteroexternal corner without definitely forming a parastyle cusp. The metastyle is likewise small and vague but is more nearly cuspidate. There is no trace of a mesostyle. The inner face of the tooth is flattened and has a distinct, median, vertical groove that divides it into two basal lobes, the posterior lobe being on  $M^1$  slightly and on  $M^2$  distinctly larger. These lobes, however, do not correspond to distinct cusps. There is only one cusp, the protocone, which is on the posterior lobe very near the distal end of the groove. Although larger, the protocone has the same structure as on  $P^4$  with the addition of a ridge to the metaconule, departing not from the apex but from the posteroexternal slope. The anteroexternal ridge, as on  $P^4$ , runs to the anteroexternal corner, or to the parastyle (here less distinct) but at its midpoint here has a cuspile, a protoconule, the

posteroexternal base of which also meets a small ridge descending the inner face of the paracone. This protoconule is very small, and the metaconule is still smaller and indistinct. The posterior crest from the protocone apex forms a sharp loop around the expanded posterointernal corner of the crown, thus making the teeth distinctly quadrate although no hypocone is present.

M<sup>3</sup> is shorter than M<sup>1-2</sup>, with the whole posterior half, most noticeably the metacone and posterointernal loop, much reduced. The internal base has only one lobe. On one specimen (9542) there is no groove, and on the other (9540) it is very slight and does not reach the base.

TABLE 30.—*Numerical data on lower teeth of Paromomys matusus*

| Variate                                | N  | R         | M           | $\sigma$    | V       |
|----------------------------------------|----|-----------|-------------|-------------|---------|
| LP <sub>4</sub> -----                  | 18 | 2.3-2.8   | 2.556±0.026 | 0.112±0.019 | 4.4±0.7 |
| WP <sub>4</sub> -----                  | 18 | 1.6-1.9   | 1.778±0.022 | 0.092±0.015 | 5.2±0.9 |
| LM <sub>1</sub> -----                  | 21 | 2.8-3.2   | 3.005±0.020 | 0.090±0.014 | 3.0±0.5 |
| WM <sub>1</sub> -----                  | 21 | 2.0-2.3   | 2.233±0.018 | 0.084±0.013 | 3.8±0.6 |
| LM <sub>2</sub> -----                  | 20 | 2.9-3.2   | 3.040±0.024 | 0.108±0.017 | 3.5±0.6 |
| WM <sub>2</sub> -----                  | 20 | 2.2-2.5   | 2.355±0.017 | 0.074±0.012 | 3.1±0.5 |
| LM <sub>3</sub> -----                  | 14 | 3.3-3.8   | 3.59±0.03   | 0.130±0.025 | 3.6±0.7 |
| WM <sub>3</sub> -----                  | 17 | 1.8-2.1   | 1.994±0.006 | 0.025±0.004 | 1.3±0.2 |
| LP <sub>4</sub> :LM <sub>1</sub> ----- | 13 | 0.77-0.89 | 0.837±0.009 | 0.034±0.007 |         |
| LM <sub>2</sub> :WM <sub>2</sub> ----- | 19 | 1.25-1.41 | 1.298±0.011 | 0.046±0.007 |         |
| LM <sub>3</sub> :LM <sub>2</sub> ----- | 10 | 1.16-1.31 | 1.215±0.014 | 0.046±0.010 |         |

TABLE 31.—*Measurements of individual specimens of Paromomys matusus*TYPE LOWER JAW<sup>1</sup>

| P <sub>4</sub> |           | M <sub>1</sub> |           | M <sub>2</sub> |           | M <sub>3</sub> |           | M <sub>1-3</sub> | LP <sub>4</sub><br>LM <sub>1</sub> | LM <sub>2</sub><br>WM <sub>2</sub> | LM <sub>3</sub><br>LM <sub>2</sub> |
|----------------|-----------|----------------|-----------|----------------|-----------|----------------|-----------|------------------|------------------------------------|------------------------------------|------------------------------------|
| L              | W         | L              | W         | L              | W         | L              | W         |                  |                                    |                                    |                                    |
| Mm<br>2.5      | Mm<br>1.7 | Mm<br>3.1      | Mm<br>2.2 | Mm<br>3.1      | Mm<br>2.3 | Mm<br>3.6      | Mm<br>1.9 | 9.0              | 0.81                               | 1.35                               | 1.16                               |

CHARACTERISTIC UPPER DENTITIONS

| U.S.N.M.no. | P <sup>4</sup> |           | M <sup>1</sup> |           | M <sup>2</sup> |           | M <sup>3</sup> |           | M <sup>1-3</sup> | LP <sup>4</sup><br>LM <sup>1</sup> | WM <sup>2</sup><br>LM <sup>1</sup> | LM <sup>3</sup><br>LM <sup>2</sup> |
|-------------|----------------|-----------|----------------|-----------|----------------|-----------|----------------|-----------|------------------|------------------------------------|------------------------------------|------------------------------------|
|             | L              | W         | L              | W         | L              | W         | L              | W         |                  |                                    |                                    |                                    |
| 9540-----   | Mm<br>2.9      | Mm<br>3.4 | Mm<br>2.9      | Mm<br>4.0 | Mm<br>2.9      | Mm<br>4.1 | Mm<br>2.3      | Mm<br>4.1 | 8.3              | 1.00                               | 1.41                               | 0.79                               |
| 9542-----   | 2.5            | 3.0       | 2.6            | 3.8       | 2.6            | 4.0       | 2.0            | 3.6       | 7.4              | 0.96                               | 1.54                               | 0.77                               |

<sup>1</sup> These measurements have been taken, and ratios calculated, on 30 different specimens, but these are most usefully summed up by the statistical data derived from them and wherever possible in this memoir I do not publish the long tables of raw measurements. Data for M<sub>1-3</sub> have not been calculated. Although at first sight this would appear to be the best single size measurement, in fact it depends to so great a degree on crushing and other extraneous factors as to be highly inaccurate and hence of little value.

The infraorbital foramen is high and narrow and lies immediately anterior to the anterior root of  $P^4$ . Very little of the orbital rim is preserved, and I see no basis for supposing it larger or smaller than in any possibly related group. It seems probable that it extended little, if any, farther forward than  $P^4$ .

The principal numerical data on lower teeth of this species are given in table 30 (see also fig. 3).

The highly homogeneous character of the sample, and by inference the only slightly variable nature of the species, is very striking. All the coefficients of variation are remarkably low and even the highest,  $5.16 \pm 0.86$ , is very commonly exceeded in races that are pure in the strictest sense.

There are too few upper jaws to calculate derived statistical data.

**PAROMOMYS DEPRESSIDENS** Gidley

FIGURE 32; PLATE 9, FIGURE 7

*Paromomys depressidens* GIDLEY, 1923, p. 4.<sup>64</sup>

*Type*.—U.S.N.M. no. 9546, part of right upper jaw with  $P^4$ – $M^3$ . Collected by A. C. Silberling.

*Horizon and locality*.—All known specimens from Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.



FIGURE 32.—*Paromomys depressidens* Gidley, U.S.N.M. no. 9485, left lower jaw, crown view. Four times natural size. (After Gidley, 1923, fig. 3.)

*Diagnosis*.—Trigonids of  $M_{1-2}$  nearly as wide as talonids.  $P^4$  less transverse than in *P. maurus*. Bases of  $M^{1-2}$  less strongly bilobed. Size notably smaller; length  $M_2$  (mean of three specimens), negative deviation from mean in *P. maurus* about eight times standard deviation of latter. See also measurements in table 33.  $P_4$  larger relative to  $M_1$ ; ratio  $LP_4:LM_1$  (one specimen), positive deviation from mean in *P. maurus* over three times standard deviation of latter.  $M_2$  wider relative to its length; ratio  $LM_2:WM_2$  (mean of three specimens), negative deviation from mean in *P. maurus* nearly three times standard deviation of latter.

*Discussion*.— $I_1$ – $P_3$  are known only from their alveoli, which are developed about as in *Paromomys maurus*. Of the two specimens showing these alveoli, one (9416) has a possible alveolus for a vestigial  $I_2$ , and the other (9482) does not, so that, as in *P. maurus*, this tooth was either absent or inconstant.  $P_4$  is slenderer and somewhat less

<sup>64</sup> In referring to Gidley's description, note that the text has been transposed. The text in Gidley, 1923, from p. 5, line 12, beginning "Several upper-jaw portions . . ." to p. 6, line 3, ending ". . . above the junction of  $P^3$  and  $P^4$ " is made part of the description of *P. depressidens* but in fact refers to *P. maurus* and evidently was meant to follow p. 4, line 12, of text, after ". . . as in *Notharctus numenius* (Cope)."



progressive than in *P. maurus*, being to some extent intermediate in structure between  $P_3$  and  $P_4$  of that species. The supposed depression of the molar trigonids, stressed by Gidley, involves slight differences that defy accurate measurement. To my eye they do not appear at all less elevated than in *P. maurus*. The trigonids of  $M_{2-3}$  are relatively slightly shorter, and the paraconids may be still more nearly connate with the metaconids. More definite is the fact that on  $M_2$  the trigonid is nearly as wide as the talonid, while in *P. maurus* it is definitely narrower. Perhaps in keeping with the smaller size, the heel of  $M_3$  is rather simple, and although it has the basic structure of *P. maurus* in some variants the third lobe is less wide and its two main cusps less distinct.

The available upper teeth of this species are all deeply worn, and I believe that the characters given by Gidley, "cusps and lophs depressed and basins shallow; protoconules present but less well defined than *P. maurus*; metaconules absent", are all due to this wear, or at least that the wear makes it impossible to know whether these are true morphological characters or not.  $P^4$  is much less transverse than in *P. maurus*, and the inner sides of the bases of  $M^{1-2}$  are less strongly bilobed. Otherwise the structure seems to be very similar, as far as it can be surely determined.

The species is decisively distinct from the genotype, and there can be no question as to its validity in spite of the fact that *P. maurus* and *P. depressidens* were absolutely contemporaneous and both are known only from the same very limited locality. These facts and the very

TABLE 32.—Measurements of known specimens of *Paromomys depressidens*

| LOWER JAWS   |                |           |                |           |                |           |                |           |                  |                     |                     |                     |
|--------------|----------------|-----------|----------------|-----------|----------------|-----------|----------------|-----------|------------------|---------------------|---------------------|---------------------|
| U.S.N.M. no. | P <sub>4</sub> |           | M <sub>1</sub> |           | M <sub>2</sub> |           | M <sub>3</sub> |           | M <sub>1-3</sub> | $\frac{LP_4}{LM_1}$ | $\frac{LM_2}{WM_2}$ | $\frac{LM_3}{LM_2}$ |
|              | L              | W         | L              | W         | L              | W         | L              | W         |                  |                     |                     |                     |
| 9485-----    | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | 7.0              | -----               | 1.11                | 1.30                |
| 9677-----    | 1.9            | 1.2       | 2.0            | -----     | 2.0            | 1.8       | 2.6            | 1.5       | 6.9              | 0.95                | -----               | -----               |
| 9482-----    | -----          | -----     | -----          | -----     | 2.2            | 1.8       | 2.7            | 1.6       | -----            | -----               | 1.22                | 1.23                |
| 9416-----    | 1.8            | 1.2       | -----          | -----     | 2.3            | 1.9       | -----          | -----     | -----            | -----               | 1.21                | -----               |
| UPPER JAWS   |                |           |                |           |                |           |                |           |                  |                     |                     |                     |
| U.S.N.M. no. | P <sup>4</sup> |           | M <sup>1</sup> |           | M <sup>2</sup> |           | M <sup>3</sup> |           | M <sup>1-3</sup> | $\frac{LP^4}{LM^1}$ | $\frac{WM^2}{LM^2}$ | $\frac{LM^3}{LM^2}$ |
|              | L              | W         | L              | W         | L              | W         | L              | W         |                  |                     |                     |                     |
| 9546-----    | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | 5.7              | 0.95                | 1.50                | 0.75                |
| 9548-----    | 1.9            | 2.0       | 2.0            | 2.6       | 2.0            | 3.0       | 1.5            | 2.7       | -----            | -----               | 1.47                | 0.68                |
| 9549-----    | -----          | -----     | 2.1            | 2.5       | 1.9            | 2.8       | 1.3            | 2.2       | -----            | -----               | 1.57                | 0.71                |
| -----        | -----          | -----     | -----          | -----     | 2.1            | 3.3       | 1.5            | 2.7       | -----            | -----               | -----               | -----               |

marked specific distinction suggest that complete, unworn dentitions might prove generic distinction, but the material actually in hand does not warrant such a conclusion.

As the samples are small, measurements of all known specimens are given in table 32 (see also fig. 3).

#### Genus and Species Undetermined

##### Cf. *PAROMOMYS*

In 1932 Silberling and I found at Loc. 13 a single left  $M^1$ , apparently representing an otherwise unknown primate. It resembles *Plesiadapis anceps* but not very exactly and is still less like other species of that genus. It is probably too small to belong to *Plesiadapis rex*, which occurs at the same locality. It resembles *Paromomys maturus* more closely than any other species with which comparison has been made, but it is more transverse, has the inner face even longer and more sloping, and has the anterointernal, not posterointernal, basal part definitely more projecting. It also resembles the most primitive species of *Pelycodus* but could not belong in that genus. Such an isolated tooth is inadequate for generic, or even for certain family identification, but its presence seems worth recording.

#### Genus *PALAECHTHON* Gidley

*Palaechthon* GIDLEY, 1923, p. 6.

*Type*.—*P. alticuspis* Gidley.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Dental formula probably  $\frac{2. 2. 2. 3}{1. 1. 3. 3}$ . Lower incisor and canine about as in *Paromomys*, or possibly incisor slightly larger and canine slightly smaller. Roots of  $P_2$  less divergent or incompletely divided.  $P_4$  larger relative to  $M_1$ , talonid as in *Paromomys*, but trigonid with distinct, subequal paraconid and metaconid. Molar trigonids very similar to *Paromomys* but on  $M_{2-3}$  paraconid slightly more distinct, lower on the crown, and less marginal.  $M_3$  with double hypoconulid, but third lobe less strong than in *Paromomys*. Trigonids more elevated. Upper molars somewhat more transverse than in *Paromomys maturus*, internal bases less distinctly bilobed, and posterointernal expansion less marked.

#### *PALAECHTHON ALTICUSPIS* Gidley

PLATE 7, FIGURE 1; PLATE 9, FIGURES 5, 6

*Palaechthon alticuspis* GIDLEY, 1923, p. 6.

*Type*.—U.S.N.M. no. 9532, right lower jaw with  $P_2$ – $M_2$ . Collected by A. C. Silberling.

*Horizon and locality.*—All known specimens from Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—Sole known species of genus as redefined. See morphological and numerical data (table 33).

*Discussion.*—From their alveoli, in two specimens (9532 and 9534),  $I_1$  and C are much as in *Paromomys maurus*, but the incisor is perhaps relatively a little larger and the canine still smaller, its alveolus occupying distinctly less space than the alveoli of  $P_2$ . There is no evidence of a second incisor.

The alveoli of  $P_2$  are confluent, and in one specimen the roots are fused, in another barely separate.  $P_2$  and  $P_3$  are similar to each other and to those of *P. maurus*.  $P_2$  is slenderer and slightly higher than  $P_3$  and  $P_3$  has the incipient anterior cuspule more nearly distinct than  $P_2$ .

$P_4$  is much more progressive than in *Paromomys*, having small but distinct subequal paraconid and metaconid in all cases, whereas in *Paromomys* these cusps are either barely incipient or entirely absent on  $P_4$ . The talonid and general structure are, however, as in *Paromomys*.

$M_1$  almost exactly resembles that of *P. maurus*.  $M_{2-3}$  are also closely similar but have the paraconid more distinct than is usual in *Paromomys*, lower on the crown and also a little more external, or less marginal. On both  $M_1$  and  $M_2$  the trigonid is nearly as wide as the talonid. On  $M_{1-3}$  the trigonid is more elevated than in *Paromomys*, and the external cingulum is weak or absent on the talonid. The third lobe of  $M_3$  is much less developed than in *Paromomys maurus*, but the hypoconulid is bifid or, in one case (9430) approximately trifid.

The mandible is also much as in *Paromomys*. In one specimen (9450) most of the posterior part is present, although the ends of the three processes are broken. The inner face is nearly plane. The coronoid is broad and apparently rose little above the articular process. Its anterior border is nearly straight and at right angle to the alveolar border. The condyle is far above the molar level. The large dental foramen is far posterior to the teeth, beneath the corono-condylar notch, and is above the alveolar level. The angle is long, slender, styloform, and thickened, and extends backward and slightly downward. Its tip was posterior to a vertical from the condyle.

$P^4$  is not known, but it has three roots and was nearly as wide as  $M^1$ . The upper molars closely resemble those of *Paromomys maurus* except in being somewhat more transverse, with slenderer sharply pointed cusps, and in the much less marked posterointernal expansion and basining. There is an internal vertical groove, but on  $M^1$  the base is not bilobed and on  $M^2$  this is barely indicated. Several of these points are resemblances to *Paromomys depressidens*, and it has already been noted that the teeth on which that species is based are much worn and of doubtful detail. As the two species are of about



the same size, the status of these upper jaws is dubious, although the lower jaws are quite distinct, and it is unfortunate that one type is an upper jaw and the other a lower. The upper jaws are, however, probably distinct and correctly associated with the lower jaws as determined by Gidley. Those placed in *Palaechthon alticus* are very slightly smaller, molars definitely more transverse, and the posterointernal basin probably less developed. It seems justifiable, in the absence of definite evidence to the contrary, to accept the identifications established and thus avoid changing the nomenclature, considering the separation of the species and genera as validated by the lower jaws and, for the present, overlooking the fact that one type is, in fact, an upper jaw and of doubtful status.

TABLE 33.—Numerical data on *Palaechthon alticus*

| Variate                              | N  | R         | M           | $\sigma$    | V       |
|--------------------------------------|----|-----------|-------------|-------------|---------|
| LM <sub>1</sub> -----                | 10 | 1.9 -2.1  | 2.030±0.025 | 0.078±0.017 | 3.8±0.9 |
| WM <sub>1</sub> -----                | 9  | 1.5 -1.7  | 1.567±0.022 | 0.066±0.016 | 4.2±1.0 |
| LM <sub>2</sub> -----                | 12 | 1.9 -2.2  | 2.067±0.024 | 0.085±0.017 | 4.1±0.8 |
| WM <sub>2</sub> -----                | 11 | 1.5 -1.8  | 1.682±0.025 | 0.084±0.018 | 5.0±1.1 |
| LM <sub>2</sub> :WM <sub>2</sub> --- | 11 | 1.17-1.40 | 1.231±0.021 | 0.070±0.015 |         |

TABLE 34.—Individual measurements of *Palaechthon alticus*

## TYPE AND CHARACTERISTIC LOWER JAWS

| U.S.N.M. no. | P <sub>4</sub> |           | M <sub>1</sub> |           | M <sub>2</sub> |           | M <sub>3</sub> |           | M <sub>1-3</sub> | $\frac{LP_1}{LM_1}$ | $\frac{LM_2}{WM_2}$ | $\frac{LM_3}{LM_2}$ |
|--------------|----------------|-----------|----------------|-----------|----------------|-----------|----------------|-----------|------------------|---------------------|---------------------|---------------------|
|              | L              | W         | L              | W         | L              | W         | L              | W         |                  |                     |                     |                     |
|              | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> |                  |                     |                     |                     |
| 9532-----    | 1.9            | 1.2       | 1.9            | 1.5       | 2.0            | 1.7       | 2.4            | 1.3       | 6.5              | 1.00                | 1.18                |                     |
| 9430-----    | 2.1            | 1.2       | 2.1            | 1.6       | 2.1            | 1.7       | 2.4            | 1.3       | 6.5              | 1.00                | 1.24                | 1.14                |
| 9483-----    | 2.0            | 1.2       | 2.1            | 1.5       | 2.1            | 1.6       | 2.3            | 1.4       | 6.3              | 0.95                | 1.31                | 1.09                |

## UPPER JAWS (ONLY TWO ARE KNOWN)

| U.S.N.M. no. | M <sup>1</sup> |           | M <sup>2</sup> |           | M <sup>3</sup> |           | M <sup>1-3</sup> | $\frac{WM^2}{LM^2}$ | $\frac{LM^3}{LM^2}$ |
|--------------|----------------|-----------|----------------|-----------|----------------|-----------|------------------|---------------------|---------------------|
|              | L              | W         | L              | W         | L              | W         |                  |                     |                     |
|              | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> |                  |                     |                     |
| 9550-----    | 1.9            | 3.0       | 1.7            | 3.0       | 1.3            | 2.5       | 5.3              | 1.76                | 0.76                |
| 9551-----    | 1.9            | 3.0       | 1.9            | 3.2       |                |           |                  | 1.68                |                     |

## Genus PALENOCHTHA Simpson

*a lenochtha* SIMPSON, 1935d, p. 231.

*Type*.—*Palaechthon minor* Gidley.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Dental formula probably  $\frac{? . ? . ? . 3}{1 . 1 . 2 . 3}$ . Anterior lower dentition shorter than in *Paromomys* or *Palaechthon* and apparently with one tooth absent, probably  $P_2$ .  $P_4$  of about the same length relative to  $M_1$  as in *Palaechthon alticuspsis* but relatively higher, with no sign of the metaconid and only vague rudiment of the paraconid.  $M_{1-2}$  similar to those of *Palaechthon*, but  $M_3$  with smaller third lobe and single hypoconulid. Upper molars similar to those of *Paromomys* and *Palaechthon* but very slender, transverse, and more triangular. Posterointernal expansion weak. Inner base not bilobed.  $M^3$  shorter relative to  $M^2$ .

*Discussion*.—In describing *Palaechthon minor*, Gidley (1923, p. 8) said: "Most of the differences noted above suggest for the species just described a slightly different line, or direction, of development than is indicated in *P. alticuspsis*. It is possible, therefore, that more complete materials may prove that these two species do not form a natural generic group." Although more complete materials are still lacking, I do not see how this species can be placed in *Palaechthon*. The further reduction of the anterior teeth, the absence of a metaconid and of a distinct paraconid on  $P_4$  (not explicitly mentioned by Gidley), and the single hypoconulid on  $M_3$  are just such differences as are used to distinguish genera among all early primates. While it is true, as Gidley notes, that the upper molars differ less from *Palaechthon alticuspsis* than do the lowers, still the differences are rather more marked than are those between the latter species and *Paromomys depressidens*. Unfortunately, the anterior upper teeth, which often show more marked generic characters, are unknown, but I think there can be no doubt that the genus is distinct.

PALENOCHTHA MINOR (Gidley)

FIGURE 33; PLATE 10, FIGURE 1

*Palaechthon minor* GIDLEY, 1923, p. 7.

*Type*.—U.S.N.M. no. 9639, right lower jaw with  $P_4$ – $M_3$  and anterior alveoli. Collected by A. C. Silberling.

*Horizon and locality*.—All known specimens from Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of the genus as described above. See description below and measurements in table 35.

*Discussion*.—Teeth anterior to  $P_4$  are represented only by alveoli in the type and in no. 9631. Both show an alveolus for a large, somewhat compressed, procumbent incisor, followed by a smaller, more erect alveolus, evidently for a canine. Between this and  $P_4$  there appears to be only a small double alveolus, or two very small alveoli confluent at their mouths. It is highly probable that this lodged one tooth,  $P_3$ , and in this event  $P_{1-2}$  must have been missing. There

appears, however, to be no diastema, and the antemolar region of the jaw is relatively shorter than in the other genera here considered, whatever may have been the exact number and homologies of the teeth.

$P_4$  is relatively higher, slenderer, and simpler than in *Palaechthon*. In the two available specimens there is no clear trace of a metaconid, and the paraconid is represented only by a very rudimentary and scarcely visible angulation of the anterior edge. The heel is short but is relatively broad and has a rudimentary basin and two very small and poorly differentiated posterior cuspules.



FIGURE 33.—*Palenochtha minor* (Gidley), U.S.N.M., no. 9590, left upper molars, crown view. Four times natural size. (After Gidley, 1923, fig. 4.)

$M_{1-2}$  are almost identical in structure with those of *Palaechthon*. The trigonid of  $M_3$  is also closely similar, but the talonid is different. It is reduced, more pointed posteriorly, with the third lobe decidedly narrower and less clearly differentiated, and the hypoconulid apparently single.

In the upper dentition, only  $M^{1-3}$  are now known. These are basically similar to those of *Palaechthon* but give quite a different superficial impression by reason of their more delicate structure, more transverse and triangular outline, and the accentuated forward twist of the protocone, present in the other primate genera but here most strongly developed. Parastyle and metastyle are distinct and subequal, as are protoconule and metaconule. The inner face of the protocone is flattened and bears a faint vertical depression, but the base is not at all bilobed. The posterointernal basin or expansion is only faintly indicated, less developed than in the other genera.  $M^3$  is short, rather strongly triangular, and developed analogously to that of *Palaechthon*.

TABLE 35.—*Individual measurements of Palenochtha minor*

TYPE AND PRINCIPAL REFERRED LOWER JAWS

| U.S.N.M. no. | $P_4$     |           | $M_1$     |           | $M_2$     |           | $M_3$     |           | $M_{1-3}$ | $\frac{LP_4}{LM_1}$ | $\frac{LM_2}{WM_2}$ | $\frac{LM_3}{LM_2}$ |
|--------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|---------------------|---------------------|---------------------|
|              | L         | W         | L         | W         | L         | W         | L         | W         |           |                     |                     |                     |
|              | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> |           |                     |                     |                     |
| 9639.....    | 1.3       | 0.8       | 1.3       | 1.1       | 1.3       | 1.2       | 1.5       | 0.9       | 4.3       | 1.00                | 1.08                | 1.15                |
| 9631.....    | 1.1       | 0.7       | 1.2       | 1.0       | 1.3       | 1.0       | -----     | -----     | -----     | 0.92                | 1.30                | -----               |
| 9636.....    | -----     | -----     | 1.3       | 1.0       | 1.3       | 1.1       | 1.4       | 0.9       | 4.3       | -----               | 1.18                | 1.08                |

UPPER JAWS (ALL KNOWN)

| U.S.N.M. no. | $M^1$     |           | $M^2$     |           | $M^3$     |           | $M^{1-3}$ | $\frac{WM^2}{LM^2}$ | $\frac{LM^3}{LM^2}$ |
|--------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|---------------------|---------------------|
|              | L         | W         | L         | W         | L         | W         |           |                     |                     |
|              | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> | <i>Mm</i> |           |                     |                     |
| 9590.....    | 1.3       | 2.0       | 1.2       | 2.0       | 0.8       | 1.6       | 3.8       | 1.67                | 0.67                |
| 9595.....    | -----     | -----     | 1.4       | 2.0       | -----     | -----     | -----     | 1.43                | -----               |



## Family CARPOLESTIDAE Simpson, 1935

As was pointed out in describing *Carpolestes* (Simpson, 1928, p. 10), *Elphidotarsius* supplies a good morphological ancestry for the very peculiar and aberrant genera *Carpodaptēs* Granger and Matthew of the Tiffany and *Carpolestes* Simpson from Tiffany or slightly later equivalents in the Fort Union. The present opportunity to compare the genotypes of the three genera at first hand fully confirms this and leaves no doubt that they are closely related.

*Elphidotarsius* and *Carpolestes* show the same highly characteristic basic structure throughout  $P_4$ - $M_3$ . *Carpodaptēs* has  $P_4$  more enlarged than in *Elphidotarsius*, its apical cuspules all in a straight line and one more in number. On  $M_1$  the trigonid is still more elongate, and the paraconid almost directly anterior to the protoconid. Other structural distinctions are very slight and unimportant. In *Carpolestes*  $P_4$  is still larger, its cuspules increased to seven or eight, its heel elevated to the trigonid level of  $M_1$ . On  $M_1$  the paraconid and protoconid are exactly in the same longitudinal line and continue without a break the cuspule series of  $P_4$ . The structural sequence *Elphidotarsius*-*Carpodaptēs*-*Carpolestes* is almost perfect (also in the size of the known species) and may be a direct phylogeny, although the possible age difference between the last two genera seems too small to permit such a marked structural advance in a direct descendant, and it is more likely that some collateral evolution is involved.

Upper teeth are as yet known only in the genera *Carpolestes* (*Carpolestes dubius* Jepsen; see Jepsen, 1930a) and *Carpodaptēs*. The molars are of primitive tritubercular type, with distinct hypocone, more or less closely paralleled in some primitive Eocene primates (e. g., *Omomys*, *Caenopithecus*, *Pseudoloris*, and others).  $P^{3-4}$ , however, are very extraordinary and unlike anything known in any other primate or indeed any placental mammal, to such a degree that when the first isolated example of one of these teeth was found I hesitantly referred it to the Multituberculata ("*Litotherium*"<sup>65</sup> Simpson, 1929, p. 9), and this remarkably bad guess was only corrected when Jepsen found associated premolars and molars. Like the last premolar of *Ptilodus*, both  $P^3$  and  $P^4$  have three longitudinal rows of cusps.

These premolars are much unlike those of any tarsiod, as is  $P_4$ , but it may confidently be predicted that  $P^{3-4}$  of *Elphidotarsius*, when found, will distinctly approach the normal tarsiod type, as does  $P_4$  of that genus.  $P^{3-4}$  of *Carpodaptēs* are indeed closer to *Carpolestes*, but they show some approach to more normal structure.

<sup>65</sup> A strict synonym of *Carpolestes* Simpson, 1928. The retention of *Carpolestes* as the definitive name is not only preferable, as Jepsen suggests, but also the only possible course in accordance with the rules of nomenclature.

The dental formula is also most completely known in *Carpolestes dubius*, in which it is  $\frac{2.2.3.3}{1.1.3.3}$ ,<sup>66</sup> as in *Paromomys*. The incisor is enlarged but does not extend beneath  $P_4$ , also as in *Paromomys*, but the canine is more reduced. In both *Carpolestes* and *Carpodaptes*  $P_{2-3}$  are reduced to 1-rooted vestiges with buttonlike crowns.

Noting these divergent specializations, but also the strong hint of tarsioidlike upper molars, in the most specialized genus of the phylum in characters not known in *Elphidotarsius*, we may expect the latter to cast more light on affinities as far as its more scanty remains go.  $P_4$  in this genus could easily be derived from one like that of, say, *Palaechthon*, but it is already too specialized, and its structural ancestor must have been too generalized, to cast any real light on affinities.  $M_1$  also shows what may be taken as the beginning of a narrowly phyletic specialization in its elongate trigonid. Otherwise it is much like that of many tarsioids but of too generalized a heritage to give decisive evidence.  $M_{2-3}$  are almost exactly like those of *Pronothodectes*, so much so that were this form known from those teeth alone it would have to be defined as a species of *Pronothodectes*. They also resemble to a marked degree those of Eocene primates of other groups, such as *Omomys vespertinus* and, in less degree, *Pelycodus*. As far as I know they do not so closely resemble any genus not now considered as primate. The characters that are distinctive from the most generalized tuberculosectorial pattern and that are not clearly habitus characters or otherwise neomorphs of this very restricted phylum all appear to me to be definitely primate. To this extent I cannot agree with Jepsen (1930a, p. 523—he was, however, dealing only with the much more aberrant terminal genus *Carpolestes* and had not recognized the relationship to *Elphidotarsius*) that “it is possible to select suites of characters which, taken by themselves, would place *Carpolestes* in any one of several orders.” I do, of course, recognize that a really definitive determination of affinities is in such cases practically impossible from teeth alone, but since teeth are, in fact, all we have I see no useful alternative to classifying them at least tentatively as belonging to the group they most resemble, that is, to the Primates.

The family in which these related, aberrant animals are placed was defined and discussed in revising the Tiffany fauna (Simpson, 1935c).

#### Genus ELPHIDOTARSIUS Gidley

*Elphidotarsius* GIDLEY, 1923, p. 10.

*Type*.—*E. florencae* Gidley.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Three lower molars and at least one premolar, dental formula otherwise unknown.  $P_4$  enlarged, equaling or exceeding  $M_1$  in

<sup>66</sup> Jepsen writes  $\frac{1.0.4.3}{1.1.3.3}$ . It is, of course, impossible to say which is correct, but the form I give seems to me slightly more probable, and it facilitates comparison by being consistent with the other formulae here used.

every dimension. Apex with four cuspules, second highest, first three anteroposterior, and fourth slightly internal. Talonid very short, with one cusp.  $M_1$  with elongate trigonid, paraconid far from metaconid, no trigonid basin.  $M_{2-3}$  with closed trigonid basins and paraconid small, near metaconid, but distinct. Talonid of  $M_3$  with well-differentiated third lobe, posterointernal rim elevated and vaguely including two or more apices. Protoconid reduced on  $M_{2-3}$ . Trigonid cusps all well in from the margin.

ELPHIDOTARSIVS FLORENCAE *Gidley*

## PLATE 10, FIGURES 2, 2a

*Elphidotarsius florencae* GIDLEY, 1923, p. 10.

*Type*.—U.S.N.M. no. 9411, left lower jaw with  $P_4$ - $M_3$ . Collected by Dr. J. W. *Gidley*.

*Horizon and locality*.—*Gidley Quarry*, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus as diagnosed above. See also description and measurements below.

*Discussion*.— $P_4$  is a very peculiar tooth, longer, wider, and higher than  $M_1$  although not greatly exceeding the latter in any dimension. Both sides are almost smoothly convex, but the apex is formed by four cuspules, or serrations, of which the second is highest although the third is slightly larger. The first three are in a straight anteroposterior line, the fourth slightly more internal. The very short heel has one cusp, from which a small sharp crest descends vertically along the posteroexternal edge of the tooth and turns into the external cingulum.

On  $M_1$  the distinct but small paraconid and the larger metaconid are widely separated and there is no trigonid basin. The metaconid is posterointernal to the protoconid. In the talonid the hypoconulid cannot be distinguished and the basin is not completely closed, as there is a deep narrow notch between the entoconid and the trigonid. On  $M_2$  the trigonid is much shorter and wider, the metaconid less posterior, the paraconid close to the metaconid although still distinct, a small trigonid basin present. The talonid is like that of  $M_1$  but larger. The trigonid of  $M_3$  is like that of  $M_2$ . The heel is modified by the addition of a well-differentiated third lobe, the elevated posterior and posterointernal rim of which shows some tendency to split into two cusps, although these are not distinctly developed. On  $M_1$  the protoconid and metaconid are of nearly equal height. On  $M_2$  the protoconid is slightly and on  $M_3$  decidedly lower than the metaconid.

To an even greater degree than is common in primitive mammals the alveolar border slopes outward, so that the external faces of all the cheek teeth are much higher than the internal.

Presumably an enlarged incisor was present, but its root did not extend under  $P_4$ , and the jaw is broken off at this point.



Measurements of the only known specimen are as follows: Length  $P_4$ , 1.5; width  $P_4$ , 1.2; length  $M_1$ , 1.2; width  $M_1$ , 1.2; length  $M_2$ , 1.2; width  $M_2$ , 1.3; length  $M_3$ , 1.7; width  $M_3$ , 1.0;  $M_{1-3}$ , 4.4; ratio length  $P_4$  : length  $M_1$ , 1.25; ratio length  $M_2$  : width  $M_2$ , 0.95; ratio length  $M_3$  : length  $M_2$ , 1.42.

#### Family PLESIADAPIDAE Trouessart, 1897

Although quite distinctive and manifestly in the plesiadapid line, *Pronothodectes* shows a definite resemblance to the other primate genera in this fauna. *Elphidotarsius* represents the beginning of a divergent line, especially in the first stages of specialization of  $P_4$ , but there is a remarkably detailed resemblance in the molar structure. The paraconids are more distinct in *Elphidotarsius* and the trigonid of  $M_1$  more expanded anteroposteriorly. The talonid cusps of  $M_{1-2}$  are less distinct. Except for the here very slight difference in the paraconid, the highly characteristic  $M_3$  is almost identical in the two genera. The resemblance to *Paromomys*, especially *P. depressidens*, in the lower teeth is also very marked, the noteworthy differences aside from the divergent emphasis in the anterior teeth being in the somewhat more progressive, or slightly different, specialization of the molar trigonids and the aberrant heel structure of  $M_3$  of *P. depressidens*. The trigonid structure, but not that of the heel of  $M_3$  is somewhat more closely approached in *Palaechthon*.

The very incomplete knowledge of *Pronothodectes* upper teeth suggests a basic resemblance to those of other genera here described, but makes it easier to see a few outstanding differences: the better paracone-metacone separation and strong conule of  $P^4$  and the less-marked posterointernal molar expansion in *Pronothodectes*, all of which are resemblances to *Plesiadapis*.

There can be no question that Gidley was right in considering *Pronothodectes* as closely related to *Plesiadapis* ("Nothodectes"). The principal differences are clear from the description. *Pronothodectes* has the enlarged incisor less procumbent, tooth reduction considerably less advanced and diastema not developed, cheek teeth less depressed and of somewhat simpler detail. In all these respects and also in the smaller size of its species, *Pronothodectes* is more primitive than *Plesiadapis*, to which it seems surely to be ancestral in a structural, and perhaps also in a literal sense.

*Pronothodectes* represents the earliest known member of a primate phylum analogous to the *Elphidotarsius*-*Carpodaptes*-*Carpolestes* phylum but with a greater known range in space and time. Its principal terms are *Pronothodectes*, middle Paleocene of North America, *Plesiadapis*, upper Paleocene of North America and Europe and, probably, lower Eocene of North America, and *Platychoerops*, lower Eocene

of Europe. The European *Cheiromyoides* Stehlin is a contemporary and close relative of *Plesiadapis*.

*Nothodectes* Matthew is clearly a synonym of *Plesiadapis*, as pointed out by Teilhard and accepted by all subsequent students.<sup>67</sup> Jepsen (1930 and 1934) tentatively placed *Plesiolestes* in this group, but the belief that it does not belong here has already been expressed above. He also (1934, p. 290) rejects my redefinition (Simpson, 1929c) of *Platychoerops* and its separation from *Plesiadapis*, but I have already defended this at some length (1935c).

*Cheiromyoides* Stehlin, accepted as valid by Abel, Jepsen, and others but rejected as a synonym of *Plesiadapis* by Teilhard, differs less from typical *Plesiadapis* than does typical *Platychoerops*. It evidently represents an only slightly divergent and, as far as known, sterile side branch of the phylum.

### Genus PRONOTHOECTES Gidley

*Pronothodectes* GIDLEY, 1923, p. 12.

*Type*.—*P. matthewi* Gidley.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Dental formula  $\frac{2.2.2.3}{2 \text{ or } 1.1.3.3}$ . Lower incisor much enlarged, semiprocumbent, root laterally compressed. Canine (or possibly  $P_1$ ) small, slightly procumbent.  $P_2$  1-rooted.  $P_4$  with quadrate base, short, high trigonid portion, no paraconid or metaconid. Talonid large with a single cuspule. Paraconid distinct on all molars, anteroexternal to the metaconid and progressively nearer the latter from  $M_1$  to  $M_3$ . No metastylid, but a vague cusp on the hypoconid-trigonid crest.  $M_3$  with third lobe and elevated postero-internal rim with two or more poorly differentiated apices.  $P^4$  with separate subequal paracone and metacone apices, their bases confluent, large conule mass, and strong protocone, which is, however, less expanded than in *Plesiadapis*. Upper molars *Plesiadapis*-like but simple, without major crenulations or secondary cuspules, and probably lacking the mesostyle (although this may be removed by wear in the known material).

### PRONOTHOECTES MATTHEWI Gidley

PLATE 8, FIGURE 1; PLATE 9, FIGURES 2, 11, 12; PLATE 10, FIGURES 3, 3a

*Pronothodectes matthewi* Gidley, 1923, p. 12.

*Type*.—U.S.N.M. no. 9547, part of right maxilla with  $P^4$ - $M^2$ . Collected by A. C. Silberling.

*Paratypes*.—U.S.N.M. no. 9332, left lower jaw with incisor root and crown of ?C,  $P_2$ ,  $P_4$ , and  $M_{1-3}$ . Collected by Dr. J. W. Gidley.

<sup>67</sup> It is, however, certain that *Nothodectes gidleyi* Matthew is specifically distinct from the European *Plesiadapis triscuspidens* Gervais.

U.S.N.M. nos. 10005 and 10044, isolated upper incisors (pertinence dubious). Collected by A. C. Silberling.

*Horizon and locality.*—All known specimens from Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—Sole known species of genus. See also description below.

*Discussion.*—The lower dentition is crowded, with no diastema.  $I_1$  is a very large, laterally compressed, nearly procumbent tooth. Its crown is not known. Immediately above and behind the root of  $I_1$  is a shallow, very small, and somewhat doubtful alveolus, probably for a vestigial  $I_2$ . The following tooth, probably a reduced canine, is also small and 1-rooted. The root is slightly procumbent, the rather formless crown more so, as it projects obliquely upward and forward from the root.

While Dr. Gidley did not discuss these anterior teeth, he gave the dental formula as  $\frac{1.1}{1.1} \text{ or } \frac{0.4.3}{0.4.3}$ , from which he evidently considered the first alveolus as doubtful and the tooth just mentioned as a first premolar. While the question cannot be answered definitely, the formula  $\frac{2}{2} \text{ or } \frac{1.1.3.3}{1.1.3.3}$  seems to me much more probable. The morphology is indecisive, but in later plesiadepids  $P_1$  are always lacking and in probably related groups (especially the tarsioids) are apparently among the first teeth to be lost, while the canine is more tenacious, being still present in the upper, although not in the lower, jaw of the much more advanced genus *Plesiadapis* and seldom or never absent in the tarsioids even though it may be reduced.<sup>68</sup>

$P_2$  is a simple tooth with one vertical root and a slightly procumbent crown excavated on the inner side and with a small 1-cusped heel.  $P_3$  has two roots and is not reduced relative to  $P_4$ . Its crown is not known.  $P_4$  is similar to that of *Plesiadapis*, but its base is more quadrate, the trigonid portion is relatively shorter and higher, the heel is at least as large, relatively, or a little larger, but its transverse posterior crest rises to one apex, rather than two as usual in *Plesiadapis*.

The paraconid is distinct on all the molars and is anteroexternal to the metaconid. From  $M_1$  to  $M_3$  it is progressively closer to the metaconid and relatively smaller. The protoconid is about as high as the metaconid on  $M_1$ , and on  $M_2$  is somewhat and on  $M_3$  much lower than the metaconid. The talonids of  $M_{1-2}$ , which are considerably wider than their trigonids, are simple and basined. A hypoconulid can be distinguished but is poorly differentiated. There is also a poorly developed cusp on the crest from the hypoconid to the posterior base of the trigonid. The entoconid-metaconid crest is notched. There is no metastylid.  $M_3$  is distinguished by the expansion of the posterior end and the development of an elevated posterointernal rim, into

<sup>68</sup> Gidley gives the formula  $\frac{?2.71}{?2.71} \text{ or } \frac{0.74.3}{0.74.3}$  for the upper dentition, but this is presumably an inference as no specimens show anything more than that there were three upper molars and at least one premolar.



which enter entoconid and hypoconulid and on which other, variable cuspules are probably developed, although obscured by wear on the known specimens.

The horizontal ramus of the mandible resembles that of *Plesiadapis*, but the symphysis (and incisor) are less inclined, and the constriction at the diastema of *Plesiadapis* is absent, as is the diastema. The larger anterior mental foramen is beneath  $P_2$  and the smaller posterior foramen beneath  $P_4$ .

The single upper jaw fragment referable to this species has only  $P^4$ - $M^2$ , and these are much worn and somewhat corroded.  $P^4$  has the paracone and metacone as well separated as in *Plesiadapis*, a large conule mass usually considered a protoconule in this group, but from its central position it could be either this or a metaconule, and a distinct protocone apparently higher but less expanded than in *Plesiadapis*. The molars seem to resemble those of *Plesiadapis* closely but to be somewhat simpler, with few or no secondary cuspules and crenulations. The anterointernal corner is more evenly rounded, not emarginate. No mesostyle can be seen. It may have been removed by wear, but probably was absent.

TABLE 36.—*Individual measurements of Pronothodectes matthewi*

## LOWER JAWS (ALL KNOWN)

| U.S.N.M. no. | $P_4$            |                  | $M_1$            |                  | $M_2$            |                  | $M_3$            |                  | $M_{1-3}$ | $\frac{LP_1}{LM_1}$ | $\frac{LM_2}{WM_2}$ | $\frac{LM_3}{LM_2}$ |
|--------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|-----------|---------------------|---------------------|---------------------|
|              | L                | W                | L                | W                | L                | W                | L                | W                |           |                     |                     |                     |
| 9332.....    | <i>Mm</i><br>1.8 | <i>Mm</i><br>1.6 | <i>Mm</i><br>2.0 | <i>Mm</i><br>2.0 | <i>Mm</i><br>2.0 | <i>Mm</i><br>2.1 | <i>Mm</i><br>3.1 | <i>Mm</i><br>1.8 | 7.3       | 0.90                | 0.95                | 1.55                |
| 9531.....    | 1.8              | 1.6              | 1.9              | 1.9              | 2.0              | 2.1              | 3.2              | 2.1              | 7.3       | 0.95                | 0.95                | 1.60                |
| 9443.....    |                  |                  | 2.1              | 2.0              | 2.1              | 2.3              | 3.1              | 2.1              | 7.4       |                     | 0.91                | 1.48                |
| 9847.....    | 1.7              | 1.9              | 2.1              | 2.0              |                  |                  |                  |                  |           | 0.81                |                     |                     |

## UPPER JAW (UNIQUE SPECIMEN)

| U.S.N.M. no. | $P^4$            |                  | $M^1$            |                  | $M^2$            |                  | $\frac{LP^4}{LM^1}$ | $\frac{WM^2}{LM^2}$ |
|--------------|------------------|------------------|------------------|------------------|------------------|------------------|---------------------|---------------------|
|              | L                | W                | L                | W                | L                | W                |                     |                     |
| 9547.....    | <i>Mm</i><br>1.9 | <i>Mm</i><br>2.7 | <i>Mm</i><br>2.0 | <i>Mm</i><br>3.2 | <i>Mm</i><br>2.1 | <i>Mm</i><br>3.5 | 0.95                | 1.67                |

## Genus PLESIADAPIS Gervais, 1877

## PLESIADAPIS REX (Gidley)

## PLATE 9, FIGURES 4, 13

*Tetoniux rex* GIDLEY, 1923, p. 11.

*Type*.—U.S.N.M. no. 9828, isolated  $M_2$ . Collected by A. C. Silberling.

*Horizon and locality.*—Loc. 13,<sup>69</sup> Fort Union, Upper Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—A poorly characterized species with  $M_2$  very low and broad. Dimensions of type  $M_2$ , 3.7 by 3.6 mm.<sup>70</sup>

*Discussion.*—Gidley compared this isolated tooth in a broad way to *Absarokius* and *Tetonius*, but his reference to *Tetonius* was clearly intended to be merely provisional. The resemblance exists, of course, but is not exact, and the tooth more nearly resembles  $M_2$  of *Plesiadapis*, which was poorly known to Gidley when he was working on these primates. This is a more probable reference, although it cannot be definitive on the basis of one tooth. The size is slightly, but significantly, larger than for  $M_2$  of *P. gidleyi*, and the crown is slightly lower. There is a closer resemblance to *P. anceps* of the Searritt Quarry, but the crown has a broader, blunter aspect.

A lower incisor figured by Gidley (1923, pl. 3, fig. 13)<sup>71</sup> probably belongs to this species. It very closely resembles the corresponding tooth of *P. gidleyi*.

Among the specimens found by Silberling and me at Loc. 13 in 1932 are two probably referable to this species. One is a right  $M_1$ , like that of *P. anceps* except for its wider lower aspect and stronger external cingulum. It measures 3.3 by 3.1 mm. The other is an upper incisor also resembling that of *P. anceps* but considerably heavier and wider relative to its labiolingual diameter, the lateral apical cusp large and directed more laterally, and with marked rugosities and small secondary cuspsules on its lingual face. There is also a slightly smaller but otherwise almost identical tooth from this locality in the Princeton collection.

When I described *Plesiadapis anceps*, from a lower level near Loc. 13, I was not aware that *Tetonius rex* Gidley belonged (in all probability) to *Plesiadapis*. The species may be synonymous, in which

<sup>69</sup> This was published as from Loc. 12 and bears that datum on the label, but it seems certain that this is not the locality in sec. 30, T. 6 N., R. 15 E., which we relocated in 1932 and which Mr. Silberling then noted as Loc. 12. In the first place, he records only invertebrates, no mammals, from that locality. In the second place, it is low in the Fort Union No. 3, and less than 550 feet above the Gidley Quarry, stratigraphically, whereas Gidley's published and manuscript data say "nearly 4,000 feet higher in the beds than in the 'Gidley Quarry' and 'Silberling Quarry' levels", which is approximately true of Locs. 11 and 13. In the third place, Gidley's data give locality "No. 12" in sec. 22, T. 5 N., R. 14 E., and Loc. 13, but not Silberling's Loc. 12, is in that section. Loc. 11 was formerly thought also to be in that section, but in 1932 it was relocated as across the line in section 23. In the fourth place, we found other material apparently of the same species at Loc. 13, and at no other horizon or locality. And finally, Dr. Gidley himself seems to have been in some doubt about this locality, for on a label of some other material he has noted "No. 12 (?13)", whereas there could hardly be any question about the distinction between the localities now recognized as 12 and 13, since they are at widely different horizons and far from each other in the field. It seems certain that the true type locality of this species is either Loc. 13 or Loc. 11 and highly probable that it is 13, although this point does not matter as 11 and 13 are near each other and at the same level.

<sup>70</sup> Gidley gives 3.8 by 3.5 mm, which is as close an agreement as is probable in measurements by different workers. I have thought best in all cases to give my independent measurements, so that they are more likely to be comparable throughout this paper.

<sup>71</sup> The figure is of the outer side of the tooth, peculiarly oriented, and is not very characteristic. The legend gives 12 as its locality, but the label says "12 (?13)", and for the reasons already given I am confident that it is really from Loc. 13, at least as they are now numbered.

case *P. rex* (Gidley) has long priority. If, however, all the material described above belongs to *P. rex*, it is almost surely distinct from *P. anceps*, and even if this is not the case it is not certain from the types that they are the same. In any event it is preferable to retain the name *P. anceps* for the present, as it is a well-known and well-characterized species, whereas *P. rex* is as yet very poorly known and its specific characters are not really established. The difference in stratigraphic level between the horizons of the two types is nearly a thousand feet.

## Order TAENIODONTA Cope, 1876

### Family STYLINODONTIDAE Marsh, 1875

Matthew (Pale. Mem.) is followed in referring all taeniodonts to a single family (with four subfamilies). This is an extremely rare group in this fauna, with only four specimens in the National Museum collection.

#### Subfamily CONORYCTINAE Matthew, 1937 (Conoryctidae Wortman, 1896)

##### Genus CONORYCTES Cope, 1881

##### CONORYCTES COMMA Cope, 1881

##### FIGURE 34

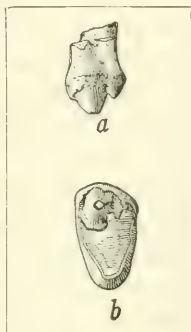


FIGURE 34.—*Conoryctes comma* Cope, U.S.N.M. no. 9597, upper molar: a, External view; b, crown view. Natural size.

Wortmann and Matthew recognized only one species of *Conoryctes* in the Torrejon, and as far as I know none has ever been described from any other formation. U.S.N.M. no. 9597, an isolated upper molar from the Gidley Quarry; no. 9678, isolated P<sup>3</sup> from the Silberling Quarry; and no. 9816, two upper molars from Loc. 6, seem to be indistinguishable from Torrejon specimens. No. 9826, from Loc. 28, a higher level, may belong to *Conoryctes* but is not determinable.

#### Subfamily PSITTACOTHERIINAE Matthew, 1937<sup>72</sup>

##### Genus PSITTACOTHERIUM Cope, 1882

##### PSITTACOTHERIUM MULTIFRAGUM Cope, 1882

Douglass (1908, p. 22) recorded a *Calamodon* in the Fort Union, querying the generic reference. Matthew (1914, p. 390) commented on Douglass' published data that this material "agrees better with *Psittacotherium*." In the National Museum collection there is a specimen, no. 6162, from the level of and near the Silberling Quarry, which includes parts of two canines, two complete cheek teeth, and other

<sup>72</sup> Matthew (Pale. Mem.) places the calamodonts and stylinodonts in the Stylinodontinae and separates the psittacotheres as a distinct subfamily.



fragments. This agrees very closely with Torrejon specimens referred to *Psittacotherium multifragum*, and judged from his figures and descriptions the same is true of Douglass' single tooth. The generic reference is beyond doubt, and the specific reference highly probable.<sup>73</sup> The species is surely and the genus probably different from ?*Psittacotherium lodbelli* Simpson, 1929, from Bear Creek, which is definitely more advanced.

## Order CARNIVORA Vicq d'Azyr, 1792

### Suborder CREODONTA Cope, 1875

Matthew has repeatedly discussed and carefully defined this primitive carnivore suborder, which includes all known Paleocene carnivores. The only serious criticism that has been made of his general arrangement (for instance by Wortman or Osborn) is that the Miacidae, being structurally ancestral to the Fissipedia, should be placed in the latter group. This would be in accord with phylogenetic classification, but as Matthew protested and as most students must agree, a completely phylogenetic classification is a practical impossibility. This case is one in which departure from it seems desirable and necessary. The Miacidae have many characters allying them with creodonts and cutting them off from their descendants the fissipedes and furthermore if they are removed from the Creodonta that group ceases to exist not only as Cope defined and conceived of it but also as a natural and practical group. Matthew's retention of the "horizontal" unit Creodonta, including the Miacidae, seems sound and is adopted here.

In the Paleocene there are five typical groups of creodonts: Oxyclaeninae, Arctocyoninae, and Triisodontinae (these three subfamilies forming the Arctocyonidae), Mesonychidae, and Miacidae (Viverravinae only in the Paleocene).<sup>74</sup> Of these the Oxyclaeninae are far the most primitive, without carnassial teeth and with decidedly generalized dentition and skeleton. The Arctocyoninae are also primitive and indeed intergrade with the Oxyclaeninae but are generally larger forms with flat, broad, bearlike teeth. The Triisodontinae are without shearing teeth but with peculiar blunt, heavy, and extremely simple teeth (probably secondarily in part). The Mesonychidae, so aberrant that they have been excluded from the Carnivora (Gregory) although probably belonging there (Matthew), developed a pseudotriciconodont and semihomodont lower dentition and are still more strikingly

<sup>73</sup> The Torrejon specimens show great variation, and Cope named three species, which were, however, considered synonyms by Wortman. Matthew (Pale. Mem.) believed it possible that more than one species occurs there but did not redefine them separately.

<sup>74</sup> Other groups begin to appear before the nominal end of the Paleocene, but they seem to be Eocene forerunners, not typically Paleocene mammals.

characterized by some strangely ungulatelike limb characters. The Miacidae had typical carnassials as in fissipedes and were generally progressive and adaptive.

All five groups are rather abundantly represented in the Torrejon in individuals, although only the Oxycloeninae there show much variety in genera and species. In the present fauna the Oxycloeninae are also abundant and varied, relatively about as in the Torrejon, although all the species and most of or all the genera are here different. The Arctocyoninae are not abundant but are apparently more varied than in the Torrejon. Triisodonts, common Torrejon fossils, are absent in this fauna as now known, and the mesonychids are represented only by extremely rare fragments. Miacids, on the other hand, are present and are more varied than in the Torrejon.

### Family ARCTOCYONIDAE Murray, 1866 <sup>75</sup>

This is one of the groups so largely and adequately defined and discussed in Matthew's memoir that redefinition here is quite unnecessary. The genera placed in the Arctocyonidae have commonly been distributed in the Oxycloenidae, Triisodontidae, and Arctocyonidae since Scott (1892) defined the first two families.

Osborn and Earle (1895) also proposed a family Chriacidae, but this was rather a substitution for Oxycloenidae (because they considered *Oxycloenus*, proper, as *incertae sedis*) than a separation from it. Matthew (1897) provisionally proposed the use of Chriacidae for *Chriacus*, "*Protochriacus*" (*Loxolophus*), and *Tricentes* if, as he then suspected, *Oxycloenus* were referable to the Triisodontidae. The latter step was not taken. *Oxycloenus* and *Triisodon* were eventually placed by Matthew in the same family, Arctocyonidae, but *Chriacus* was also placed there. The earlier work adumbrated a fourfold division, with groups typified by *Oxycloenus*, *Chriacus*, *Arctocyon*, and *Triisodon*. Various of these were at times separated widely, but the way in which some genera were shifted from one to another and all sorts of combinations made shows how hard it really is to tell these groups, or supposed groups, apart.

In his latest work, Matthew (Pale. Mem.) took the logical step of reuniting all these genera under the oldest family name, Arctocyonidae. It seems to be demonstrated that all are rather closely related and

<sup>75</sup> I would prefer to give, and in some earlier publications have given, as author of a family the first writer who recognized the group and gave it a name based on a valid genus, even if he did not follow the family form now maintained. This would make Giebel, who named the Arctocyoninae in 1855, author of the Arctocyonidae. In fact he was, aside from quibbling, for his group Arctocyoninae was distinguished from *nonarctocyonids*, not from *other arctocyonids* (none of which were then known) and was, as far as then possible, the group we now call Arctocyonidae. In reality, then, Giebel is the author of this family, but the bibliographers will not have it so and, of course, they are correct in the letter of the law, if not in a spirit of justice. On the grounds of literal correctness and largely of feeling that the purpose of quoting authority is not to honor but only to define, I have abandoned my former practice. This statement applies to a number of other groups as well as to this.

even if the supposed groups are separable, they do not all together exceed the usual limits of a single family of carnivores.

Matthew subdivides the family into Oxyclaeninae, Chriacinae, Arctocyoninae, and Triisodontinae. These are essentially the old families, except that the Chriacidae of Osborn and Earle and (tentatively suggested, not adopted) of Matthew was merely the Oxyclaenidae with *Oxyclaenus* excluded, while the Chriacinae of Matthew's last work is based on quite a different concept and includes only *Chriacus* and *Deltatherium*.

Despite the name of the family, its central, most varied, and most typical group is that of the Oxyclaeninae. Separation of the Triisodontinae seems justified, since these animals (not yet identified in the present fauna) are of a peculiar adaptive type only the earliest examples of which show close approach to oxyclaenines. The Arctocyoninae form a clear-cut group if contrasted with such types as *Oxyclaenus* or *Chriacus*, but such genera as *Protogonodon*, *Tricentes*, *Arctocyonides*, or *Thryptacodon*, each in a different way, tend to bridge the morphological gap and to make clear differentiation difficult or impossible. Perhaps in the fanlike radiation of this potent and extremely varied family several lines approached a bearlike, omnivorous adaptive type and the Arctocyoninae may be a partly artificial concept uniting several of the more extreme adaptive types independently trending in this direction. Despite this possibility, the concept is a practical one and may well be adopted pending a better understanding of the actual phylogeny.

The idea of separating *Chriacus* from the Oxyclaeninae seems less fortunate, and it is probably impractical at present. The Arctocyonidae with the Triisodontinae and Arctocyoninae removed are a hodgepodge including many different lines each potentially or actually as distinct as that suggested by *Chriacus*. These numerous minor phyla are so intricately interrelated and most of them are so poorly known that a good subfamily or supergeneric arrangement is not now attainable. It does not seem helpful to separate one genus, *Chriacus*, which is probably no more distinctive than each of a dozen others. From another viewpoint the inadequacy of such an arrangement is also shown by the discovery of such a type as *Metachriacus*, which might roughly be characterized as "chriacine" in premolars and "oxyclaenine" in molars. With the greatest respect for Matthew's incomparable knowledge of these faunas and clearness of judgment it further seems to me that his collocation of *Deltatherium* is based on superficial characters and that this genus differs more from *Chriacus* than does any of several genera not placed in the Chriacinae.

The present fauna contains certainly six and possibly seven genera of Arctocyonidae. Five of these were defined from this fauna and have not definitely been recognized elsewhere. Of the Crazy Moun-



tain arctocyonids, *Claenodon* belongs in the Arctocyoninae. *Deutero-gonodon* might be placed there or in the Oxyclaeninae, or even in the Condylarthra. In default of better evidence and for ease of subfamily recognition it is placed in the Arctocyoninae, which it most resembles in adaptive characters although perhaps not phyletically close to other members of that group.

*Mimotricentes* is a typical but well-differentiated oxyclaenine. *Prothryptacodon* seems surely to be in the lineage of *Thryptacodon*, with which it forms a rather distinctive phylum retained in the Oxyclaeninae, where *Thryptacodon* has generally been placed. *Meta-chriacus* is an oxyclaenine in the broad sense. If Oxyclaeninae and Chriacinae were separated, this genus would be *incertae sedis*, for it resembles both groups. *Spanoxyodon* is also clearly oxyclaenine, *sensu lato*, and might doubtfully be an aberrant chriacine if that group were retained. The occurrence of *Chriacus* in the fauna is possible, but not proved, and no additional evidence on the affinities of that genus is here adduced. *Coriphagus*, with which the Torrejon *Mixoclaenus* is synonymous, was classified by Matthew in the Oxyclaeninae, but I believe it to be an anisonchine, as set forth in dealing with that group.

The members of this family are the most primitive of known carnivores, and, as might be expected, they are abundant in all Lower and Middle Paleocene faunas. In the Upper Paleocene they are less varied and common, and as far as known they died out by the end of lower Eocene time. The Middle Paleocene forms are prototypal in a general, structural sense, but are already too late to be ancestral to other groups. Matthew (Pale. Mem.) has pointed out the great interest of the family as probably including in its Lower Paleocene or, especially (unknown), pre-Paleocene members the probable ancestry not only of all carnivores but also of other orders, including most or all ungulates and some others. Despite the numerous minor structural modifications, most members of the family have almost diagrammatic tuberculo-sectorial teeth such as are believed to be primitive for all marsupial and placental mammals. The osteological characters of the group as a whole are also primitive for the great majority of placental mammals, many of them for all these, but on these characters the present materials have practically nothing to add to what is known from the Puerco and Torrejon mammals.

#### Subfamily ARCTOCYONINAE Giebel, 1855

*Claenodon* and *Deutero-gonodon* represent this subfamily in the present fauna. The status of a supposed third genus, *Neoclaenodon*, is discussed below. *Deutero-gonodon* might be considered an oxyclaenine, in view of its resemblance to *Protogonodon*, which Matthew so classi-

fies, but its adaptive characters, at least, are more arctocyonine and the groups are more easily defined if it is placed here. It may not really be a creodont.

#### Genus *CLAENODON* Scott

*Claenodon* SCOTT, 1892, p. 298.

Synonym: *Neoclaenodon* Gidley, 1919.

This group was studied by Dr. Gidley and the results published (1919), his manuscript notes including no further observations. One specimen, of considerable interest, has since been added to the National Museum collection (by Silberling and me in 1932), and there are several specimens in the Princeton collection that were not included by Gidley in his publication. Dr. Gidley also studied Cope's types and at least two later American Museum Torrejon specimens (A. M. nos. 16543 and 16545), but he apparently did not examine the whole American Museum series, which includes about 50 specimens. On this basis I am forced to adopt a broader view of the variability of the group and to modify the generic and specific criteria used, thus arriving at a modified systematic arrangement, which also differs from the final conclusions of Dr. Matthew (Pale. Mem.), based on American Museum material only.

With one exception, the Fort Union specimens were all referred by Gidley to a new genus, *Neoclaenodon*. The supposed generic characters as given by Gidley (1919, p. 547) may be listed and commented on as follows:

1. "Cranial portion of skull relatively long and deep; interorbital space apparently much narrower, and postorbital constriction longer and more slender than in *Claenodon*." This is based on a comparison of two specimens, one of *Claenodon* "*corrugatus*" and one of "*Neoclaenodon*" *montanensis*, as no others yet discovered show these features. They are crushed in opposite ways, which accounts for part of the difference in aspect. This individual of "*N.*" *montanensis*, however, probably does have a slenderer and longer midcranial region, but this is a character so variable with age, so likely to be of merely specific value at best, and so impossible to use on a practical basis for the separation of the fossil species that, in itself, it does not carry generic weight.

2. "Anterior premolars, upper and lower, much reduced; in upper jaw distinct diastemae behind  $P^1$ , and between  $P^2$  and  $P^3$ ; the first premolar, above and below, lies closely appressed to the canine." This is in part distinctive from some specimens of *C. ferox*, and not from others. The influence of selecting particular specimens for comparison is seen in the fact that Matthew (Pale. Mem.) proposed to redefine *Neoclaenodon* as having the premolars *unreduced* [relative to *Claenodon*]. In fact the whole series with its various species is variable in these characters and varies, as far as apparent, about a

single mode. These premolar characters are certainly not generic and probably not good specific characters.

3. "Hypocone in  $M^1$  and  $M^2$  rudimentary." This is a fairly clear distinction from any Torrejon specimen known to me. The species *montanensis* may be distinguished by having the hypocones of  $M^{1-2}$  slightly smaller than the smaller variants of other known species. If this be made a generic character, however, it would be almost the sole character defining the genus and the genus would be monotypic, as even Gidley's "*Neoclaenodon*" *silberlingi* probably had hypocones proportionately as in the larger species.

4. "Hypocone . . . wanting in  $M^3$ ;  $M^3$  much reduced, suboval in outline with relatively small metacone." This again applies only to a very limited extent to "*N.*" *silberlingi*. Furthermore, in the Torrejon species usually (but incorrectly) called *C. protogonioides* some specimens have *corrugatus*-like  $M^3$  and others that are, nevertheless, surely conspecific have  $M^3$  almost as in "*N.*" *montanensis*. *C. ferox* has relatively larger  $M^3$ , but the hypocone is often lacking. The character is obviously somewhat variable and when well marked of specific, not generic, character.

5. Various skeletal characters (all repeated in the extended description quoted below) are also given. Here it need only be said that, as Gidley points out, the basic structure is quite as in *Claenodon*. Some characters, as the fusion of scaphoid and centrale (not, however, considered diagnostic by Gidley) or the broad astragalus (which was considered diagnostic), although apparently fundamental, are individually variable in *C. ferox*. None is more important than the slight structural modification to be expected in smaller and larger species of one genus.

Matthew (Pale. Mem.) accepts *Neoclaenodon* as probably valid but rejects all Gidley's characters as not being diagnostic of the genus. He does not clearly redefine it but mentions its smaller size, unreduced premolars, and lack of heavily rugose enamel. The smaller size (about 25 percent) is surely not a generic character. The supposed difference in premolar reduction is probably subjective, as already suggested: Matthew says the premolars are less reduced than in *Claenodon*, and Gidley says they are more reduced. They seem to me to be about the same, taking each supposed group as a whole. The rugosity of the enamel is about the same proportionately in "*N.*" *montanensis* as in *C. ferox* but is probably less in *C. "protogonioides."*

Matthew's acceptance of *Neoclaenodon* is based on the Torrejon species that has generally been called *Claenodon protogonioides*. This name is not applicable in this way, as it belongs to a Puerco species (probably of the genus *Protogonodon*), and Matthew proposes a new name (Pale. Mem., unpublished at the time this was writ-



ten). He places the species in *Neoclaenodon* and bases his ideas of *Neoclaenodon* on it, apparently overlooking the fact that this would exclude its own genotype from this genus. Indeed "*N.*" *montanensis* resembles *Claenodon ferox* in several points, which are differences from the Torrejon species hitherto confused with *protogonioides*, such as the more rugose enamel, the stronger and crenulated cingula, and the shelf-like, rather than conical, protocone on P<sup>4</sup>. On this basis the small Torrejon species might (but in my opinion should not) be placed in a new genus, but the genus would not be *Neoclaenodon*.

Thus, while there are single characters on which genera might be founded, none of these seems either well marked or highly significant, nor are they combined in such a way as to support the separation of *Claenodon* and *Neoclaenodon* as proposed either by Gidley or by Matthew. The upshot of using such characters would be to force the erection of a genus for each well-defined species, a procedure not useful and concordant with the really close resemblance of all members of this group.

The species previously recognized or proposed are as follows:

*Claenodon ferox* (Cope, 1883). Genotype.

*C. corrugatus* (Cope, 1883).

*C. sp. innom.* (Matthew, Pale. Mem.) = "*C. protogonioides*", *pars*, of authors (in error). [*C. procyonoides* (Matthew, 1937); published too late to insert throughout the present bulletin.]

*C. montanensis* (Gidley, 1919). Genotype of *Neoclaenodon*.

*C. silberlingi* (Gidley, 1919).

*C. latidens* (Gidley, 1919).

Of these, I consider *C. corrugatus* as a synonym of *C. ferox*, and *C. silberlingi* and *C. latidens* as of doubtful validity, one or both possibly being synonymous with *C. montanensis*. Another species, *C. recordensis* has been described from the present fauna.

In comparing some of the Fort Union specimens with the Torrejon material and in considering the general nature and limits of variation and the validity of specific distinctions in this group, it has been necessary to restudy the Torrejon specimens. These have in the past been referred to three species, following Cope, *C. ferox*, *C. corrugatus*, and *C. protogonioides*. The type of *C. protogonioides* is from the Puerco, and Matthew (Pale. Mem.) has shown that it belongs in *Protogonodon* and that the Torrejon specimens hitherto placed there do not belong to it but to an unnamed species (named in Pale. Mem.), surely distinct from *C. ferox* or *C. corrugatus*.

*C. corrugatus* was distinguished from *C. ferox* by Cope as being smaller and with the hypocone somewhat better developed. The latter character is variable and, in the extremely slight degree indicated by the types, seems to be individual. Matthew (Pale. Mem.) considers *C. corrugatus* as of doubtful status but redefines it as smaller, with less robust premolars, inner cusps less developed on P<sup>3-4</sup>, de-

cidedly smaller and slenderer canines, limb and foot bones smaller and of slenderer proportions throughout.

I am at a loss to understand the supposed distinction of the inner cusps of  $P^{3-4}$  as I find no specimen identified by Matthew as *C. ferox* that has those teeth. The number of specimens in which the canines are surely associated with cheek teeth is limited, but the measurements and ratios shown in table 37 can be taken from the collection.

TABLE 37.—Measurements of canines and molars of species of *Claenodon*

| A.M.N.H. no. and species                             | C         | M <sup>1</sup> | $\bar{C}$ | M <sub>1</sub> | $\frac{C}{M^1}$ | $\frac{\bar{C}}{M_1}$ |
|------------------------------------------------------|-----------|----------------|-----------|----------------|-----------------|-----------------------|
|                                                      | <i>Mm</i> | <i>Mm</i>      | <i>Mm</i> | <i>Mm</i>      |                 |                       |
| 3268 (type <i>C. ferox</i> )-----                    | 12.9      | 11.1           | -----     | -----          | 1.16            |                       |
| 2456 (neotype <i>C. corrugatus</i> )-----            | 8.3       | 10.5           | 7.8       | 12.5           | 0.79            | 0.62                  |
| 16545 (ref. <i>C. corrugatus</i> )-----              | 11.2      | 10.0           | -----     | -----          | 1.12            |                       |
| 16001 <sup>1</sup> (ref. <i>C. corrugatus</i> )----- | -----     | -----          | 10.0      | 11.0           | -----           | 0.91                  |
| 3271 <sup>1</sup> (ref. <i>C. ferox</i> )-----       | -----     | -----          | 10.2      | 10.6           | -----           | 0.96                  |
| 3266 <sup>2</sup> (ref. <i>C. corrugatus</i> )-----  | -----     | -----          | 8.8       | 11.2           | -----           | 0.78                  |

<sup>1</sup> Not identified by Matthew, Pale. Mem., earlier references.

<sup>2</sup> Doubtfully referred by Matthew, Pale. Mem.

No. 3271, with the smallest cheek teeth, has the largest canine among the lower jaws, and no. 2456, with the largest cheek teeth among the lower jaws, has the smallest canine. Indeed among the lower jaws the relative canine size varies inversely with the cheek-tooth size, the exact opposite of the hypothesis on which the species are separated. Among the upper jaws the largest cheek teeth are associated with the relatively largest canine, medium-sized cheek teeth with the relatively smallest canine, and the smallest cheek teeth with relatively middle-sized (but in ratio nearer the relatively largest) canine. The samples are too small for extended statistical study, but it is quite obvious that the smaller individuals are not characterized by relatively small canines, and hence that the supposed specific distinction in this character is invalid. Beyond that no regular correlation of gross size, or cheek-tooth size, with relative canine size is suggested or possible on these data. It is suggested that canine size is extremely variable and that both large and small cheek teeth may be associated with both relatively large and small canines. There is perhaps a sexual distinction in relative canine size in addition to or instead of in absolute cheek-tooth size, but this is a hypothesis that the data are inadequate to test.

The smaller premolars and slenderer skeleton supposedly distinctive of *C. corrugatus* cannot be more exactly checked, and the results are similar: they are smaller, because they belong to smaller individuals, but there is no apparent correlation of relatively smaller premolars or relatively slenderer limbs with the smaller individuals.

The distinction thus is reduced to a matter of size. To judge this I have taken a single dimension, the length of  $M_2$ , because it seems to be a valid indication of cheek-tooth or gross individual size and can be measured in a relatively large number of individuals. Other dimensions give similar results and all need not be published here. There are in all 24 individuals of the genus *Claenodon* from the Torrejon in the American Museum collection in which the length of  $M_2$  can be measured. The small species hitherto confused with *C. protogonioides* is obviously distinct, and the following data apply only to the *C. ferox-corrugatus* group.

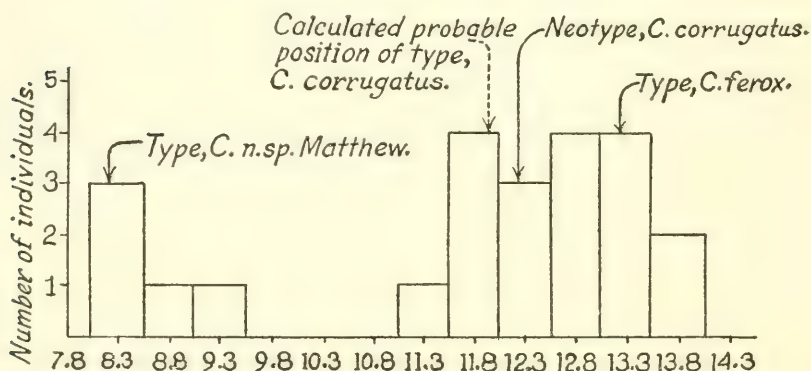


FIGURE 35.—Histogram of length of  $M_2$  of *Claenodon* from the Torrejon of New Mexico in the American Museum.

The statistical data on the length of  $M_2$  of the group are as follows:

|                          |       |              |
|--------------------------|-------|--------------|
| Number in sample         | ----- | 18           |
| Observed range           | ----- | 11.5 - 13.9  |
| Mean                     | ----- | 12.68 ± 0.25 |
| Standard deviation       | ----- | 1.06 ± 0.18  |
| Coefficient of variation | ----- | 8.3 ± 1.4    |

Contrary to some (e.g., Klähn) of the few paleontological workers who have used any statistical data but the most elementary, I cannot agree that the extent of variation ("Variationsbreite"), in this case 2.4 mm (11.5 to 13.9), has any valuable connotation, being so dependent on accidents of sampling that the probable error is enormous. The same fundamental idea is more correctly conveyed by the standard deviation. The above data are calculated from raw measurements to 0.1 mm, but in the histogram (fig. 35) these are grouped in units 0.5 mm wide, because of the small size of the sample and because 0.1 is certainly too refined a measurement and below the limits of mechanical error and errors due to crushing of the specimens, etc.



The only deflection in the frequency curve is in the 12.05–12.55 group, and this is not significant. By actual calculation, which need not be given here, a deflection at this point would have to be of at least 3 to have any probable significance, and this deflection is in fact only of 1. The mean, the median, and the mode almost exactly coincide.

The distribution thus indicates a unimodal, unskewed curve, and provides no warrant for splitting into two groups, or species, on the basis of size (or of this dimension, which is sufficiently closely correlated with size).

The actual positions of the types are indicated on the histogram. The neotype of *C. corrugatus*, although not elsewhere formally so designated, is such essentially as Matthew (Pale. Mem.) largely bases his redefinition of the species on it. The type of *C. corrugatus* has no  $M_2$ , but it must have measured about 12.0 mm in this dimension, calculated from the ratios of associated  $M^2$  and  $M_2$  in surely conspecific individuals of about the same size.  $M_2$  of the neotype of *C. corrugatus* is 12.4 mm in length and of the type of *C. ferox* 13.4 mm.<sup>76</sup> The deviations of these three specimens are: *C. ferox*, type, +0.72; *C. corrugatus*, plesiotype, -0.28; *C. corrugatus*, type, calculated, -0.68. All these deviations are considerably less than the standard deviation. There is no reason or warrant for placing these individuals in different species on the basis of size.<sup>77</sup>

The coefficient of variation, 8.34, is high and indicates a species of considerable variability in size, but there are many cases of dimensions of single species, and even of subspecies or pure races, with equally high variability, or higher, and this figure does not in itself suggest that two species, inseparable on these data, may be present.

These data do not prove that two species are *not* present: Such proof of a negative is practically impossible, and the burden of proof is always to be considered as required from the positive side. They do show that in this sample it is impossible to distinguish two size groups (and hence two species distinguished by size differences), that the distribution is not inconsistent in modality, variability, etc., with a single species, and adding considerations somewhat beyond purely statistical treatment, that if two species were present they would very probably not correspond with those now recognized.

There are no other variates or attributes, so far as I can observe, that do permit any differentiation of this group into two or more species. The supposed species occur together, at the same horizon and localities, and in approximately equal numbers.<sup>78</sup>

<sup>76</sup> It is crushed and spread a little, but this can be exactly allowed for.

<sup>77</sup> It may also be noted that on the purely hypothetical and extremely improbable supposition that two species were present and that their size limit corresponded with the deflection in the frequency curve given, the neotype of *C. corrugatus* would belong with *C. ferox* and the type of *C. corrugatus* would be on the boundary between the two groups.

<sup>78</sup> This, of course, depends on individual identifications, but if these were to be based on any rational size distinction the grouping would have to be into two approximately equal groups.

In short, *C. corrugatus* and *C. ferox* are not distinguishable on any correct factual basis derived from the known specimens, and they must be considered synonymous, the name *C. ferox* being retained for the species. The value of the coefficient of variation may be taken as indicative of the degree of variability to be expected in the same or analogous dimensions in species of this genus.

The relationships of the genus *Claenodon* as a whole have been widely discussed and are summed up so thoroughly by Matthew (Pale. Mem.) that no details need be given here. It is a typical arctocyoniid, very close to *Arctocyon* itself, and in its larger species, at least, forerunner of the lower Eocene *Anacodon*, after which the line evidently became extinct. Relationship with the bears has often been suggested and was favored by Dr. Gidley, but it is almost certainly erroneous. There is very little question that bears developed from dogs during the Middle or Later Tertiary and that the limited convergence to them shown by *Claenodon* involves habitus characters only and denotes a convergence in food and other habits, but not any special affinity.

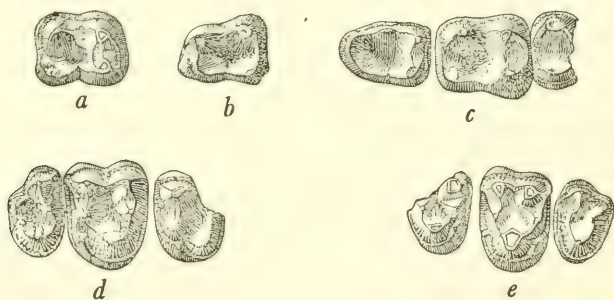


FIGURE 36.—*Claenodon ferox* (Cope), tentatively referred specimens from the Melville (Fort Union No. 3): a, U.S.N.M. no. 6156, left  $M_2$ ; b, Princeton Univ. no. 13755, right  $M_1$ , probably from Loc. 44; c, same data as b, left  $M_2-3$  and heel of  $M_1$ ; d, same data as b, right  $M_1-3$ ,  $M_1$  broken; e, Princeton Univ. no. 13756, left  $M_1-3$ ,  $M_1$  broken, probably from Loc. 49. All natural size.

#### CLAENODON FEROX (Cope, 1883)

##### FIGURE 36

U.S.N.M. no. 6156, a left <sup>79</sup>  $M_2$  and some other fragments, from well up in Fort Union No. 3, was tentatively referred by Gidley (1919, pp. 545–547) to *Claenodon ferox*, with the reservation that better material might prove that a new species is represented. Gidley noted several distinctions from characteristic *C. ferox* of the Torrejon but suggested that all could be due to individual variation, except, perhaps, the fact that in the Montana specimen the talonid is narrower than the trigonid. This, however, is also within the range of variation of *C.*

<sup>79</sup> Gidley, 1919, p. 545, says "right", obviously a *lapsus calami*.

*ferox*, and there are Torrejon specimens practically identical with that from Montana in size and structure. The specimen probably does represent *C. ferox*, but the single tooth is inadequate for certain determination. The same statement applies to no. 9651, an isolated left P<sup>4</sup>, from Loc. 53.

There are several Princeton specimens of *Claenodon* from their cluster of localities in Fort Union No. 3 near the center of the field. These all appear to represent one species, with considerable variation but not beyond that usual for this group. Morphologically they are within the limits of the *C. ferox* group and cannot be separated from that species.

#### CLAENODON MONTANENSIS (Gidley)

##### FIGURES 37-39

*Neoclaenodon montanensis* GIDLEY, 1919, p. 547.

*Type*.—U.S.N.M. no. 8362, much of the skull and jaws with most of the dentition, parts of fore and hind limbs, and other fragments. Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Sweetgrass County, Mont.

*Diagnosis*.—Gidley (1919, p. 550): "About one-fifth smaller than *Claenodon ferox* and *C. corrugatus*, slightly larger than *C. protogonioides* (Cope); face relatively short, rostrum deep; brain-case very small and elongate; postorbital constriction long and slender; posterior root of zygoma depressed below the basioccipital plane (probably a primitive character and of much more than species significance), giving a decidedly arched contour to the main portion of the skull viewed from the side; anterior border of orbit directly above anterior boundary of m<sup>2</sup>; infraorbital foramen directly above middle of p<sup>3</sup>; the large, moderately recurved, slightly compressed canines with root-portion much swollen and in contour difficultly distinguishable from the crown into which it merges without any deviation in outline; 1st premolar, upper and lower, single-rooted, relatively large (compared with p<sup>2</sup>) and closely appressed to the canine; p<sup>3</sup> and p<sup>4</sup> triangular, three-rooted, p<sup>4</sup> with incipient protocone; upper m<sup>3</sup> <sup>so</sup> suboval in outline, much reduced with low external cusps, the metacone relatively small and inwardly placed; p<sub>3</sub> and p<sub>4</sub> with small, narrow, single-cusped heels; lower jaw relatively thin and deep with the lower border of its anterior half but slightly curved.

#### "MEASUREMENTS

|                                                                     |          |
|---------------------------------------------------------------------|----------|
| Length of upper dental series, C to M <sup>3</sup> (estimated)..... | 63.1 mm. |
| Length p <sup>3</sup> to m <sup>3</sup> .....                       | 37.6 mm. |
| Length p <sup>4</sup> (estimated).....                              | 7.3 mm.  |

<sup>so</sup> The original has "m<sup>2</sup>", an obvious misprint.—G. G. S.



|                                                                        |           |
|------------------------------------------------------------------------|-----------|
| Width p <sup>4</sup> -----                                             | 7.5 mm.   |
| Length m <sup>1</sup> -----                                            | 9.4 mm.   |
| Width m <sup>1</sup> -----                                             | 10.0 mm.  |
| Length m <sup>3</sup> -----                                            | 5.5 mm.   |
| Width m <sup>3</sup> -----                                             | 9.3 mm.   |
| Length of lower dental series c to m <sub>3</sub> -----                | 65.0 mm.  |
| Length m <sub>1</sub> to m <sub>3</sub> -----                          | 28.5 mm.  |
| Length m <sub>2</sub> -----                                            | 9.4 mm.   |
| Width m <sub>2</sub> -----                                             | 7.5 mm.   |
| Length m <sub>3</sub> -----                                            | 9.9 mm.   |
| Width m <sub>3</sub> -----                                             | 6.5 mm.   |
| Depth of jaw at m <sub>2</sub> -----                                   | 21.5 mm.  |
| Depth of jaw at p <sub>2</sub> -----                                   | 18.2 mm.  |
| Total basal length of skull (estimated)-----                           | 155.0 mm. |
| Width of skull across orbital region, including zygomas (estimated)--- | 65.0 mm.  |

"Even in our present knowledge of the *Clanodont* group it is difficult to determine the limits of individual variation and species characters; and it is quite probable that some of those here stated have a much wider significance than I have given them, while others may have less importance. This statement applies equally to the following more detailed description of the type specimen.

"The skull is not greatly specialized but shows the following characteristic modifications: glenoid fossae situated forward in position as in the *Miacidae*; sagittal crest high and prominent (primitively correlated with the small brain, and the large canines with which were doubtless associated heavy temporal muscles), occipital crest but little expanded; nasals long, slightly widening forward and overlapped by a considerable portion of the maxillary in the normal creodont-carnivore way; posterior root of zygoma prominent with roof of glenoid fossae depressed below the level of basisphenoid plane as in the bears; relative position and arrangement of cranial foramina, also as in the *Ursidae*, that is, the optic foramen is placed well forward of the anterior sphenoidal fissure which lies close to the foramen rotundum, with the anterior opening of the alisphenoid canal just below them; the ethmoid foramen lies nearly above the optic foramen and well behind the postorbital process (an important character, as the position of this foramen marks the posterior border of the cribriform plate of the ethmoid); foramen ovale, and posterior opening of alisphenoid canal connected by a groove or depression which is separated from the basisphenoid plate by a prominent ridge of the alisphenoid."

*Discussion.*—Dr. Gidley also well described and figured the various known limb elements of this species. As already suggested, most of the distinctions noted by him were based on comparison with a single specimen of *Clanodon ferox*, and they disappear or seem of very little importance when more material is brought into the comparison. The proportionate widths of radial facets on scaphoid and lunar are 5.3:8.1,

or 0.65 (almost exactly two-thirds, as stated by Gidley), and in one specimen of *C. ferox* (that with which Gidley made comparisons) this ratio is 10.1:15.4, or 0.66, so that the different size, preservation, and to a slight degree proportions evidently misled his eye when he supposed the ratio to be significantly smaller in *C. montanensis*. The

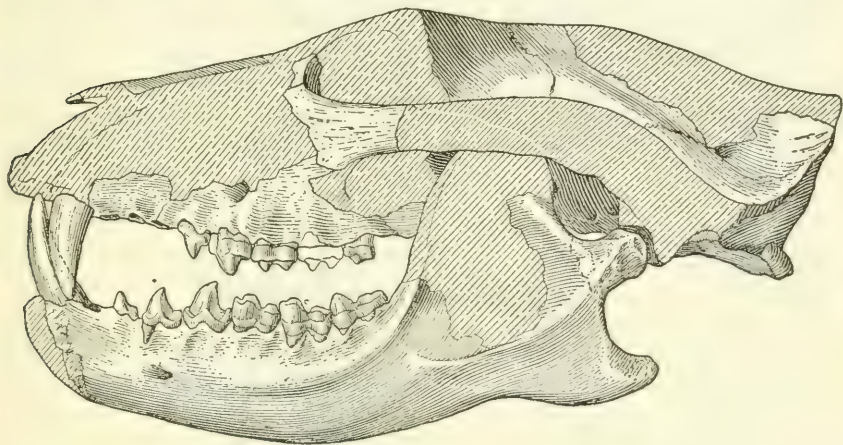


FIGURE 37.—*Claenodon montanensis* (Gidley), U.S.N.M. no. 8362, skull and jaws, left side. Three-fourths natural size. (After Gidley, 1919, fig. 5.)

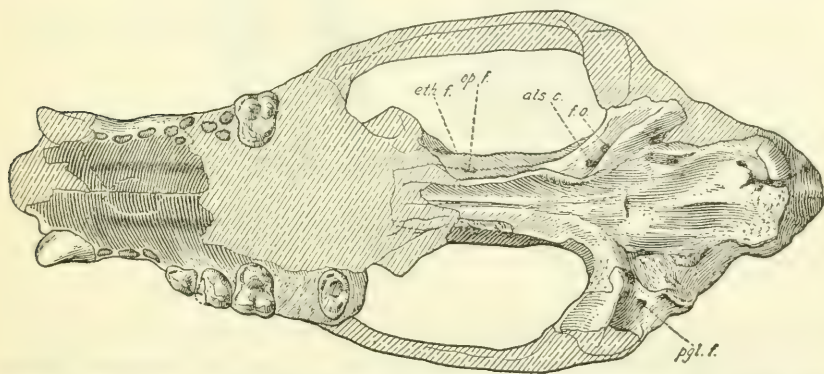


FIGURE 38.—*Claenodon montanensis* (Gidley), U.S.N.M. no. 8362, skull, palatal view. Three-fourths natural size. (After Gidley, 1919, fig. 6.)

ratio of total widths is 0.47, or about half, as stated by Gidley, in *C. montanensis* type, and 0.46 in the specimen of *C. ferox*, which again is a wholly insignificant difference. Computation of the exact figures also shows Gidley's impression that the vertical depths of the anterior faces of these bones are relatively less than in *C. ferox* to be mistaken. They are in fact slightly, but not significantly, greater than in this specimen of *C. ferox*.

In Gidley's description of the calcaneum (1919, p. 552), "tibial face" is probably a misprint for "fibular facet." The type calcaneum is somewhat damaged in this region. A specimen collected after Dr. Gidley's paper was published shows that in *C. montanensis* the fibular facet on the calcaneum is relatively quite as well developed as in *C. ferox*. His statement, "cuboid with facet for the astragalus, navicular and ectocuneiform arranged horizontally, nearly parallel and merging into each other" also appears to involve a misprint or *lapsus*, since it is inconsistent with his accurate figures and is either not clear or not correct. As his figures show, the astragalar facet is at an angle of nearly  $90^\circ$  to the navicular facet, and the latter and the ectocunei-

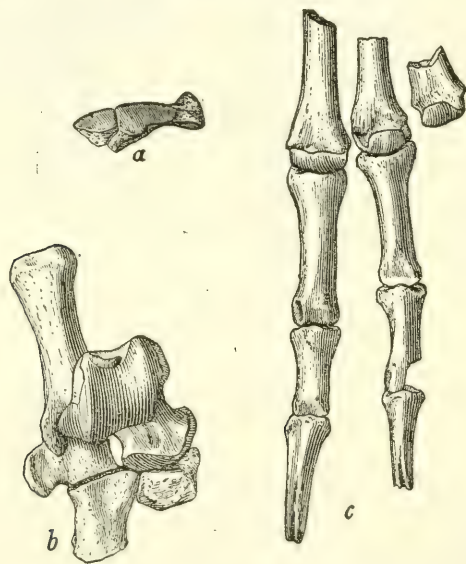


FIGURE 39.—*Claenodon montanensis* (Gidley), U.S.N.M. no. 8362, foot bones: a, Lunar and scaphoid, dorsal view; b, part of tarsus, dorsal view; c, parts of the three median digits of pes, dorsal view. Natural size. (After Gidley, 1919, figs. 7 and 8.)

form facet are approximately in the same vertical plane. Comparison of several specimens of *C. ferox* does not confirm the supposed difference in this species in the separation and different outline of the two last mentioned facets on the cuboid. These facets are much less definite in the available specimens of *C. ferox*<sup>81</sup> than in *C. montanensis*, but differ little in outline.

Dr. Gidley's important conclusion that the present limb bones are closely similar to those of *Claenodon ferox* is certainly correct and is only emphasized by these slight corrections of details. The *C. montanensis* material is little over half of the size of that of *C. ferox*, and it differs in details of proportion, strength of processes, or rugosities,

<sup>81</sup> The artist has made their outline far too distinct in Gidley, 1919, pl. 28, fig. 2a.



such as are normally specific functions of size, but not in any essential structure.

As already suggested, Dr. Gidley's comparison with *Ursus* seems to me to be beside the point and to involve no features not to be expected by convergence in heavily built plantigrades not more closely related than as members of wholly different groups of the same order.

The species is surely distinct from *C. ferox*, being excluded from that group by the smaller size, reduced hypocone of  $M^1$ , and reduced size and more transverse proportions of  $M^3$ . (Some of the other characters given by Gidley are not of probable specific value.) The size is within the probable range of the small unnamed Torrejon species. For instance, the length of  $M_2$  is 9.2 in the largest Torrejon specimen of the small species and 9.4 in the type of *C. montanensis*. The size distribution doubtless overlaps, but were a larger series available it is probable that the mean for the Fort Union specimens would be found to be significantly greater. The reduction of the posterior part of  $M^3$  is also within the extreme limit of variability of the Torrejon species but probably is a specific character varying about a different, but not widely separate, mode. The somewhat smaller hypocones of  $M^{1-2}$  and the less conical protocone of  $P^4$  seem to be beyond the limits of the Torrejon specimens and thus still better specific characters, on present data. Possibly correlated with the differences in  $P^4$  is the somewhat narrower, more distinctly unicuspid character of  $P_4$ , also apparently a good specific character.<sup>82</sup>

U.S.N.M. no. 9634 is an isolated  $M_1$  from the Gidley Quarry, measuring 9.4 by 6.5 mm and referable to this species with little doubt. No. 6159, from Loc. 52,<sup>83</sup> includes right and left  $M_2$ , apparently associated, and other fragments, also referable to *C. montanensis*.

#### CLAENODON SILBERLINGI (Gidley)

##### FIGURE 40

*Neoclaenodon silberlingi* GIDLEY, 1919, p. 552.

*Type*.—U.S.N.M. no. 8363, part of left<sup>84</sup> maxilla with  $P^3$ – $M^3$  and alveoli for canine and  $P^{1-2}$ . Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Sweetgrass County, Mont.

*Diagnosis*.—Gidley (1919, p. 553): "A slightly smaller species than *N. montanensis* from which it differs as follows: cusps of all the molars seemingly<sup>1</sup> more depressed;  $m^3$  and  $pm$ 's<sup>3,4</sup> somewhat less reduced

<sup>82</sup> These, of course, substantiate the validity of the still unpublished Torrejon species, rather than of *C. montanensis*, which has priority and is surely distinct from any species previously named.

<sup>83</sup> Labeled "'Gidley Qu.' (Recorded Loc. 'No. 52' = Loc. No. 4).'" Loc. 52 is very near the Gidley Quarry and about 50 feet lower stratigraphically. The difference does not appear to have any importance, but the localities are not exactly the same.

<sup>84</sup> "Right" in the original designation of type (Gidley, 1919, p. 552) is a *lapsus*.

<sup>85</sup> "Though found in its original bed, the enamel of all the teeth is considerably damaged through weathering or leaching by surface water which had reached the specimen through cracks in the matrix."

although more reduced than in *Claenodon*: all the cheek teeth, except  $p^3$ , relatively wider; distance between  $p^3$  and the canine relatively greater indicating a somewhat more elongate face; infraorbital foramen approaching nearer to the alveolar border above  $p^3$ .

"This species in size approximates *C. protogonioides* (Cope) but is apparently clearly distinguishable from the Puerco species by the much greater reduction and more oval contour of  $m^3$ , and in the relatively wider proportion of all the cheek teeth.

"MEASUREMENTS OF *N. silberlingi*

|                                        |          |
|----------------------------------------|----------|
| c to $m^3$ .....                       | 60.0 mm. |
| $p^3$ to $m^3$ .....                   | 34.5 mm. |
| $m^1$ to $m^3$ .....                   | 21.4 mm. |
| $m^1$ length.....                      | 7.0 mm.  |
| $m^1$ width.....                       | 8.8 mm.  |
| $m^2$ length.....                      | 7.4 mm.  |
| $m^2$ width.....                       | 11.5 mm. |
| $m^3$ length.....                      | 5.0 mm.  |
| $m^3$ width.....                       | 9.0 mm.  |
| Distance between $p^3$ and $p^2$ ..... | 5.0 mm.  |
| Height of $p^3$ (outside).....         | 5.5 mm.  |
| Length of canine alveolus.....         | 7.5 mm." |

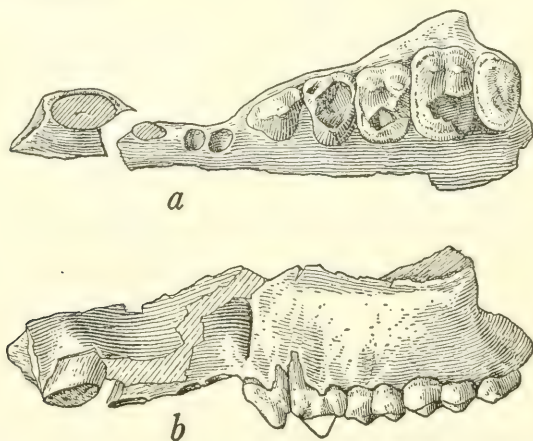


FIGURE 40.—*Claenodon silberlingi* (Gidley), U.S.N.M. no. 8363, left upper jaw: a, Crown view; b, external view. Natural size. (After Gidley, 1919, fig. 9.)

*Discussion.*—Allusion to "*C. protogonioides*" implies comparison rather with the unnamed Torrejon species of *Claenodon* than with the different Puerco species to which the name properly applies.

The type of this species is so poor, the cusp structure being very much obscured and in part destroyed by corrosion and breakage, that it cannot surely be distinguished from the small Torrejon species, on one hand, or from *C. montanensis*, on the other, although these two are distinct from each other.

The relative size and contour of  $M^3$  are, in fact, well within the range of variation of the Torrejon species, and the teeth are not significantly more transverse. The size is large for that species but not beyond its presumable range and hence of doubtful significance. It is impossible to give good clear diagnoses separating the two, although it is my opinion that they are probably distinct.

It is, on the other hand, probable that *C. silberlingi* is synonymous with *C. montanensis* (adding to the probability that it is not the same as the Torrejon species). The size is about the same, and both types are from one quarry.  $M^1$  is a little shorter in *C. silberlingi*, and somewhat more transverse, but these are doubtfully real, since the specimen is so poorly preserved, and if real are not marked enough to prove any taxonomic distinction.  $M^3$  is definitely larger than in *C. montanensis*. The ratio of their lengths, the dimension in which they differ most, is 1.10. In Torrejon specimens of the *C. ferox* group the variation in absolute dimensions is much greater than this, and the size of  $M^3$  relative to  $M^1$  or  $M^2$  also varies quite as much as the difference between *C. silberlingi* and *C. montanensis*, although this is a more constant figure.

The distance between  $P^3$  and the canine is almost exactly as in *C. montanensis*. In calling it "relatively greater", Gidley must have meant relative to the length of  $M^1$ , but as the other tooth dimensions are as great as in *C. montanensis* this is simply to repeat that the length of  $M^1$  is relatively small and is not a character of the diastema.  $M^{1-2}$  may have had larger hypocones than in *C. montanensis*, but this is almost hypothetical, and the protocone of  $P^4$  may have been stronger, also rather dubious.

I retain the name tentatively, on these very doubtful characters, but believe that the species will probably prove to be invalid.

CLAENODON LATIDENS (Gidley)

FIGURE 41

?*Neoclaenodon latidens* GIDLEY, 1919, p. 554.

*Type*.—U.S.N.M. no. 8388, right lower jaw with  $M_{2-3}$ , a small fragment of  $M_1$ , and the broken lower part of the ramus from the canine alveolus to the angle. Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Sweetgrass County, Mont.

*Diagnosis*.—Gidley (1919, pp. 554-555): "Size approximately that of *N. montanensis*, but with decidedly wider molars; jaw relatively longer, much straighter, and more slender. Since the upper dentition of *N. latidens* and the lower dentition of *N. silberlingi* are not known, these species can not now be compared, but the difference in size seems sufficient to distinguish them.



## "MEASUREMENTS

|                             |          |
|-----------------------------|----------|
| Length of $m_2$ .....       | 9.7 mm.  |
| Width of $m_2$ .....        | 8.4 mm.  |
| Length $m_3$ .....          | 9.6 mm.  |
| Width of $m_3$ .....        | 7.6 mm.  |
| Depth of jaw at $m_2$ ..... | 16.0 mm. |

"Unfortunately, as in the type of *N. silberlingi*, the enamel of the molars has been considerably damaged through weathering or leaching by surface water, which somewhat obscures the detailed structure.

"The generic reference is provisional, since certain features, as the straight and more slender proportions of the jaw and relatively greater width of the lower molars, so sharply distinguish *N. latidens* from all other species of this genus or of *Claenodon*. They suggest that its affinity to the group to which I here assign it may be, after all, not very close. More complete and better preserved material may, therefore, necessitate placing it in a distinct genus."

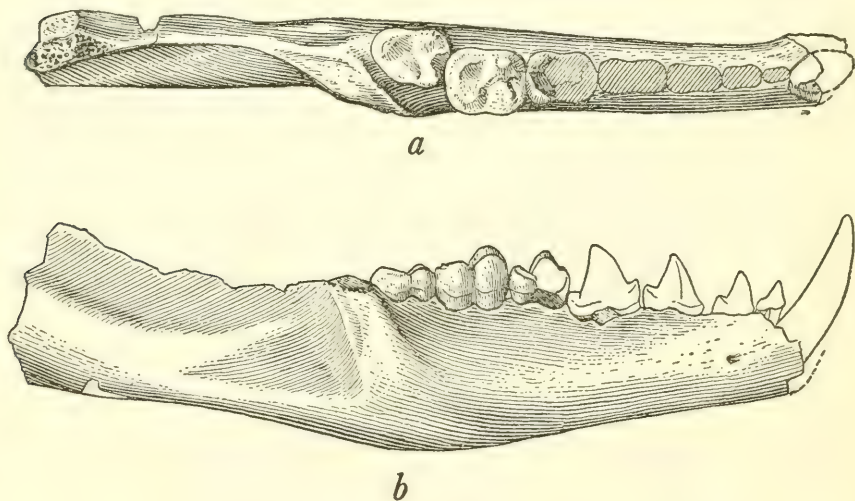


FIGURE 41.—*Claenodon latidens* (Gidley), U.S.N.M. no. 8383, with parts in outline probably adapted from other species of *Claenodon*, right lower jaw: *a*, Crown view; *b*, external view. Natural size. (After Gidley, 1919, fig. 10.)

*Discussion.*—The apparent differences from *C. montanensis* in the shape of the mandibular ramus are, in my opinion, illusory and due to the different preservation of the two specimens. The jaws appear to have been almost identical or at least well within the possible range for a single species. So far as available material goes, the species depends wholly on the notably wider  $M_{2-3}$ . That this is of specific value is not certain, especially as the size is otherwise that of *C. montanensis* and both are from the same quarry, but the species may be tentatively retained. I see no reason to suspect that a new genus is represented.

## CLAENODON VECORDENSIS Simpson

## FIGURE 42

*Claenodon vecordensis* SIMPSON, 1935d, p. 232.

*Type*.—U.S.N.M. no. 13781, left  $M^{2-3}$ . Collected by A. C. Silberling and G. G. Simpson, 1932.

*Horizon and locality*.—Loc. 9, 300 feet above the base of Fort Union No. 1, Crazy Mountain Field, Mont.

*Diagnosis*.— $M^2$  similar to that of *C. silberlingi* in outline but 10–20 percent larger and somewhat more transverse; hypocone vestigial, strong crenulated internal cingulum.  $M^3$  relatively as large as in *C. ferox* and similar in structure except for smaller metacone and more evenly rounded external border; vestigial hypocone present.

*Discussion*.—This species is smaller than the smallest known variants of *C. ferox*, has a smaller hypocone on  $M^2$ , and the contours of  $M^2$  and  $M^3$  are different and beyond the known range of variation of that species. *C. silberlingi* is somewhat smaller and has different tooth proportions.  $M^3$  is much larger and less transverse than in *C. montanensis* and has the posterior part better developed. The small unnamed Torrejon species is much smaller and has less wrinkled enamel, and the internal cingulum is feebler or absent.



FIGURE 42.—*Claenodon vecordensis* Simpson, U.S.N.M. no. 13781, left  $M^{2-3}$ , crown view. Natural size.



FIGURE 43.—? *Claenodon* sp., U.S.N.M. no. 6153, left  $M_1$ , crown view. Natural size.

It is unfortunate that another poorly known species must be added to this genus, already burdened with several species of doubtful status, but the present specimen is identifiable and surely cannot enter into any species previously established so far as their range of variation is known or can be fairly inferred. It is, furthermore, from a very different geological horizon from the other Fort Union claeonodonts and one from which little material has been obtained, so that its stratigraphic importance also necessitates some convenient designation for it.

Measurements: Length  $M^2$ , 9.0; width  $M^2$ , 13.5; length  $M^3$ , 6.7; width  $M^3$ , 10.0.

## ?CLAENODON species

## FIGURE 43

U.S.N.M. no. 6158, from the Gidley Quarry, is a left lower jaw fragment with  $M_1$ . Among Dr. Gidley's notes are two sheets devoted to a

description of this specimen, in which it is placed in a new species. Apparently it was at first placed in *Claenodon* with a query, and later the generic name was erased and another, which appears to be new, substituted, but no corresponding change was made in the description, and the genus was not defined. I do not believe this to be adequate for the definition of either genus or species and feel obliged to suppress these manuscript names. The specimen is aberrant (with respect to species of *Claenodon*) in several details, but their significance cannot be judged and comparative Fort Union material is too scanty for good diagnosis. It is, for instance, entirely possible that this belongs to *Claenodon latidens*.<sup>85</sup>

### Genus DEUTEROGONODON Simpson

*Deuteronodon* SIMPSON, 1935d, p. 232.

*Type*.—*D. montanus* (Gidley).

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Dentition basically arctocyonid in type, and resembling *Protogonodon* and *Claenodon*. Small, distinct, cingulum hypocone on  $M^{2-3}$  (at least), cingula almost completely circling these teeth. Small but well-defined mesostyle present. Parastyle of  $M^3$  a distinct cusp, crowning a lobe projecting strongly externally. Lower molars with trigonid only slightly higher than talonid, metaconid smaller than but as high as protoconid. Paraconid very small but distinct, subconical, on slope of metaconid directly anterior to its apex. Talonid basin open, crescentic lophid continuous but crest differentiated into hypoconid, hypoconulid, and entoconid, progressively smaller in that order. Enamel wrinkled, but all cusps clear-cut and little or no tendency to form crenulations or accessory cusps.

*Discussion*.—This seems to be a very distinctive genus, at once distinguished from any similar form by the presence of a mesostyle. The combination of the other characters given is equally distinctive, although individually they are less so. The genus could be a derivative of *Protogonodon*, although it is too incompletely known and too distinctive to establish this as a definite theory. I know of no Torrejon genus that compares more closely than the probably related but manifestly distinct *Claenodon*, and none of the lower Eocene arctocyonids could be derived from *Deuteronodon*. The possibility that *Phenacodus* was derived not from *Tetraclaenodon*, as commonly supposed, but from *Protogonodon* by way of a form something like *Deuteronodon* is worthy of consideration but cannot be very seriously

<sup>85</sup> Dr. Gidley may have had the same idea, and his manuscript is perhaps older than the publication of 1919. The specimen was collected before the type of *C. latidens* and was obviously in Dr. Gidley's hands when he wrote his claeodont paper, so that its omission may well be due to his having decided that the specimen did not warrant a new name.



upheld on present evidence. Aside from the presence of a mesostyle, *Deuteronogodon* is much less like *Phenacodus* than is *Tetraclaenodon*.<sup>86</sup>

Dr. Gidley's manuscript notes include two drafts of a description of the type of this genus, in both of which it is referred to *Protogonodon*. On one, however, almost surely the second, the words "new genus" have later been written under "*Protogonodon*." Gidley thus came to recognize the clear-cut distinction of this genus from *Protogonodon*, but his notes do not contain any generic diagnosis or new generic name, and I have been forced to supply these.

**DEUTEROGONODON MONTANUS (Gidley)**

FIGURE 44

*Deuteronogodon montanus* (GIDLEY) SIMPSON, 1935d, p. 233.

*Type*.—U.S.N.M. no. 6160, part of right maxilla with a fragment of  $M^1$ ,  $M^2$  lacking the paracone and parastyle, and  $M^3$  complete, with a left lower jaw fragment, possibly of the same individual and almost surely of the same species, with the talonid of  $M_1$  and most of  $M_2$ . If these should prove not to be one individual, the upper teeth constitute the type, and the lower teeth are a paratype. Collected by A. C. Silberling.

*Paratype*.—U.S.N.M. no. 6161, isolated right  $M_2$ .

*Horizon and locality*.—All material is from Loc. 25, about 300 feet above the base of Fort Union No. 2, Sweetgrass County, Mont.

*Diagnosis*.—Gidley: "Somewhat larger than *P. [Protogonodon] pentacus* (Cope)."<sup>87</sup>

Simpson: Sole known species of the genus as defined above.

Measurements are as follows:

|                              |      |
|------------------------------|------|
| $M^2$ median width.....      | 14.6 |
| $M^3$ length.....            | 10   |
| $M_2$ (paratype) width.....  | 10.5 |
| $M_2$ (paratype) length..... | 12.6 |

<sup>86</sup> A new species of *Protogonodon* from the Puerco, which I have described in a note published as a supplement to Matthew's Paleocene Memoir, suggests that within the genus *Protogonodon* there was a tendency to develop along two different lines, one leading (or related and collateral) to *Tetraclaenodon* and one more definitely creodont and *Claenodon*-like. If derived from *Protogonodon*, *Deuteronogodon* probably arose from a species of the latter, rather than of the former, group.

<sup>87</sup> I quote only enough of Dr. Gidley's diagnosis to establish his authorship of the species. The rest of the diagnosis compares with the Puerco species of *Protogonodon* and is hence rather generic than specific, and among the few characters given I cannot agree as to the reality or value of some, and others seem to involve slips of the pen that I cannot correct with any certainty that Dr. Gidley's thought is being followed. The rough manuscript was far from completion.

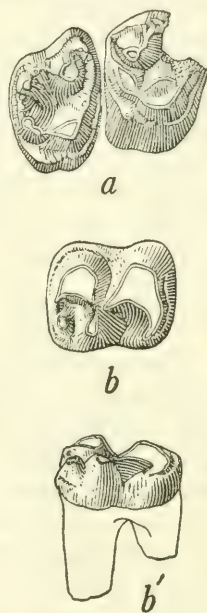


FIGURE 44.—*Deuteronogodon montanus* (Gidley): a, U.S.N.M. no. 6160, right  $M^2-3$ , crown view; b, U.S.N.M. no. 6161, right  $M_2$ , crown view; b', same, internal view. Natural size.

## ?DEUTEROGONODON species

U.S.N.M. no. 9653 includes part of a left maxilla with  $P^1-M^1$  and part of a right mandible with the heel of  $M_3$ . All the teeth are incomplete and much battered, and none is directly comparable with the types of *D. montanus*, so that pertinence to that genus and species cannot be established but is probable, at least as far as generic identity.<sup>88</sup> The principal characters exhibited are that  $P^1$  has a strong conical protocone, somewhat smaller than the external cusp or cusps, and that in the talonid of  $M_3$  the three cusps, especially the entoconid, are more distinctly separated than in  $M_{1-2}$  of the type of *D. montanus*. These specimens are from Loc. 18, the horizon of which is in doubt but is higher than that of the types of *D. montanus* and in Fort Union No. 3.

There are likewise a few tooth and limb fragments, from the type locality, that probably belong to this genus but are of no particular value at present.

Subfamily OXYCLAENINAE Matthew, 1937 (Oxyclaenidae Scott, 1892)

The oxyclaenine genera of this fauna, *Metachriacus*, *Mimotricentes*, *Spanoxyodon*, *Prothryptacodon*, and (somewhat doubtfully) *Chriacus*, belong with several other Paleocene genera in a very confusing complex. The size ranges of their species do not differ greatly, and their morphology is markedly stereotyped in general pattern. Within the limits of this general type, however, they seem to ring almost every possible change in combinations of detail, so that they are difficult to distinguish yet are amazingly varied in minutiae and cannot be grouped into one or a few broad but natural genera. The variations involve, among other features:

1. Placing of the canine (from vertical in *Tricentes*, etc., to strongly procumbent in *Prothryptacodon*, etc.).
2. Number and crowding of premolars and associated development of diastemata, varying from such types as *Metachriacus* to *Spanoxyodon*.
3. Molarization of  $P_4$ , from a wholly premolariform type, as in *Tricentes* (and several other genera) to a submolariform condition as in *Spanoxyodon*.
4. Reduction of the paraconid, from strong and distinct (e. g., *Deltatherium*) to almost indistinguishable (e. g.,  $M_{2-3}$  of *Metachriacus*).
5. Placing of the paraconids, from almost strictly internal (e. g., *Mimotricentes*) to almost strictly median (e. g., *Tricentes*).
6. Elevation of the trigonids and their shearing character, from high and strongly shearing (e. g., *Chriacus*) to low and bunodont (e. g., *Tricentes*).

<sup>88</sup> Dr. Gidley labeled them as of the same species.

7. Proliferation of accessory cuspules, from practically nil (e. g., *Chriacus*) to considerable and distantly approaching the multicuspid "arctocyonines" (e. g., *Metachriacus*).

8. Development of hypocones on upper molars from practically nil (e. g., *Deltatherium*) to pronounced (e. g., *Chriacus*).

Other characters, known in fewer genera, also seen to be highly distinctive, such as the molarization of upper premolars, width of external upper molar shelf, shape of paracone and metacone, and many other characters.

Table 38 contrasts the genera of this complex that occur in this fauna, and those most likely to be confused with them, as regards these characters.

TABLE 38.—Comparison of dentition characters in six genera of *Oxyclaeninae*

| Genus                      | Canine                                                 | P <sub>1-4</sub>          | Diastemata                                            | P <sub>1</sub>                                  |
|----------------------------|--------------------------------------------------------|---------------------------|-------------------------------------------------------|-------------------------------------------------|
| <i>Chriacus</i> .....      | Moderately procumbent.                                 | Present....               | Slight or none.....                                   | Slender, with small, distinct metaconid.        |
| <i>Metachriacus</i> .....  | Cf. <i>Chriacus</i> .....                              | .....do.....              | Cf. <i>Chriacus</i> .....                             | Cf. <i>Chriacus</i> .                           |
| <i>Tricentes</i> .....     | Crown vertical.....                                    | P <sub>1</sub> absent.... | Short, C-P <sub>2</sub> .....                         | Stouter, no metaconid.                          |
| <i>Mimotricentes</i> ..... | Cf. <i>Tricentes</i> .....                             | Present....               | None.....                                             | Cf. <i>Tricentes</i> .                          |
| <i>Spanoryodon</i> .....   | Cf. <i>Chriacus</i> .....                              | P <sub>1-2</sub> absent.. | Long, C-P <sub>1</sub> .....                          | With metaconid larger than in <i>Chriacus</i> . |
| <i>Prothryptacodon</i> ..  | Strongly procumbent, root extending beneath premolars. | Present....               | Very slight, around P <sub>1</sub> , P <sub>2</sub> . | Slender, metaconid barely incipient or absent.  |

| Genus                      | Paraconids of M <sub>2-3</sub>                                           | Trigonids of M <sub>1-3</sub>                   | Cuspules of M <sub>1-3</sub>                                                                                      | M <sub>1-3</sub>                                                                                                                                       |
|----------------------------|--------------------------------------------------------------------------|-------------------------------------------------|-------------------------------------------------------------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------|
| <i>Chriacus</i> .....      | Distinct, near metaconids, internal.                                     | Elevated, shearing.                             | No accessory cuspules.                                                                                            | With well-developed hypocones, some tendency to develop protostyles                                                                                    |
| <i>Metachriacus</i> .....  | Vestigial, placed about as in <i>Chriacus</i> or slightly less internal. | Lower than in <i>Chriacus</i> , still shearing. | Tendency to develop cuspules on anterior rim of trigonid, conules on both hypoconid wings, and slight metastylid. | Sharp cingulum around protocones of M <sub>1-3</sub> but hypocones rudimentary on M <sub>2</sub> , absent on M <sub>3</sub> , no distinct protostyles. |
| <i>Tricentes</i> .....     | Vestigial, low on crown, nearly median.                                  | Still, lower, bunodont.                         | Enamel rugose or papillate but few or no definite cuspules.                                                       | Hypocones small or absent, no protostyles.                                                                                                             |
| <i>Mimotricentes</i> ..... | Vestigial, higher on crown than in <i>Tricentes</i> and internal.        | Cf. <i>Tricentes</i> .....                      | Cf. <i>Tricentes</i> .....                                                                                        | Cf. <i>Tricentes</i> .                                                                                                                                 |
| <i>Spanoryodon</i> .....   | About as in <i>Chriacus</i> or slightly less internal.                   | About as in <i>Chriacus</i> or slightly lower.  | Cf. <i>Chriacus</i> .....                                                                                         | (Unknown.)                                                                                                                                             |
| <i>Prothryptacodon</i> ..  | Comparable to <i>Metachriacus</i> , but slightly better differentiated.  | Cf. <i>Chriacus</i> .....                       | Cf. <i>Chriacus</i> .....                                                                                         | (Unknown.)                                                                                                                                             |



Renewed study has necessitated some modification of the arrangement given in a preliminary paper (Simpson, 1935d). In the first place the species there called *Chriacus pusillus* was wrongly placed in *Chriacus*. It belongs in *Metachriacus*, where it is indistinguishable from the genotype, *M. punitor*. This makes possible some redefinition of *Metachriacus*, which proves to be even more distinct from *Chriacus* than was at first supposed. The species called *Tricentes latidens* (quoted from Dr. Gidley's notes) is now seen to be distinct from *Tricentes*, despite a very marked adaptive resemblance, for it has  $P_1$ , apparently always absent in *Tricentes*, and the paraconids are in quite a different position although reduced about as in *Tricentes*. It is necessary to erect a new genus for this species, since redefinition of *Tricentes* to include it would make that genus so broad as to destroy all balance in the generic arrangement of the family achieved by Matthew and others.

*Spanoxyodon* is a peculiar type with aberrant specialization, and *Prothryptacodon* is evidently a very primitive form slightly but definitely modified in the direction of *Thryptacodon*.

For convenience in identifying fragmentary material a summary (table 39) of lower tooth dimensions is here given.

TABLE 39.—Measurements (in mm) of lower dentition in seven species of *Oxyclaeninae*<sup>1</sup>

| Species and number of specimens           | $P_4$ |     | $M_1$ |     | $M_2$ |     | $M_3$ |     |
|-------------------------------------------|-------|-----|-------|-----|-------|-----|-------|-----|
|                                           | L     | W   | L     | W   | L     | W   | L     | W   |
| <i>Prothryptacodon furens</i> (2)-----    | 4.9   | 2.7 | 5.2   | 3.7 | 5.2   | 4.2 | 5.3   | 4.0 |
| ? <i>Chriacus pugnar</i> (1)-----         |       |     | 7.1   | 5.9 |       |     |       |     |
| <i>Metachriacus punitor</i> (9)-----      | 4.3   | 2.7 | 4.7   | 3.7 | 5.0   | 4.3 | 5.7   | 3.7 |
| <i>Metachriacus provocator</i> (12)-----  | 5.0   | 2.9 | 5.4   | 4.2 | 5.8   | 4.9 | 6.7   | 4.1 |
| <i>Spanoxyodon latrunculus</i> (1)-----   | 5.0   | 2.8 | 5.2   | 3.9 | 5.8   | 4.5 |       |     |
| <i>Mimotricentes latidens</i> (2)-----    | 5.4   | 3.9 | 5.6   | 4.7 | 6.0   | 5.5 | 6.1   | 4.7 |
| <i>Mimotricentes angustidens</i> (4)----- | 4.4   | 3.0 | 4.8   | 3.6 | 5.6   | 4.6 | 5.5   | 3.6 |

<sup>1</sup> The figures in this table are means for the number of specimens (in all, not necessarily for every dimension) shown in parentheses. The range of variation is known reasonably well only in *Metachriacus punitor* and *M. provocator*, as given hereinafter. The dimensions in themselves are not necessarily distinctive, for instance between *Metachriacus provocator* and *Spanoxyodon latrunculus*, but in such cases there are, of course, well marked nonnumerical distinctions. Some worn and incomplete specimens might, however, be unidentifiable in such cases.

### Genus PROTHRYPTACODON Simpson

*Prothryptacodon* SIMPSON, 1935d, p. 233.

*Type*.—*Prothryptacodon furens* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Canine semiprocumbent, root extending beneath premolars, as in *Thryptacodon*.  $P_{1-2}$  spaced widely.  $P_4$  similar to *Thryptacodon*. Molar trigonids higher than in *Thryptacodon*, para-

conids reduced and in nearly the same position as in *Thryptacodon* but more distinct, higher on crown, trigonids less basined, and with fewer accessory cuspules. Only one distinct inner talonid cusp (entoconid), as opposed to two in *Thryptacodon*.

*Discussion*.—This genus could well be ancestral to *Thryptacodon* and in any case is evidently allied to it. The adaptive characters are somewhat intermediate between the more primitive types, such as *Oxyclaenus*, and the more complex type seen in *Thryptacodon*, involving some flattening of the molar crowns and proliferation of cuspules. In these characters *Thryptacodon* and to a less extent *Prothryptacodon* parallel or converge toward the *Claenodon*–*Anacodon* line. The latter group, however, is much earlier and more highly specialized in this rather bearlike direction. *Prothryptacodon* is contemporaneous with *Claenodon* in the Middle Paleocene, and *Claenodon* is already more specialized than *Thryptacodon* in this direction. *Thryptacodon* appears in the Upper Paleocene and survives into the lower Eocene, where *Anacodon* appears as a highly aberrant survivor of the *Claenodon* group.

The canine is slender, laniary, compressed, with the root considerably larger than the crown and meeting the latter at an angle of about  $135^{\circ}$ . The root is implanted almost horizontally and extended at least to the anterior end of  $P_2$ .  $P_1$ , from its alveolus, had a single root and was well spaced, slightly nearer to the canine than to  $P_2$ .  $P_2$  and  $P_3$  were 2-rooted, and  $P_2$  is preceded and followed by a short diastema.  $P_4$  has a very slight internal swelling, high on the crown, that may indicate an incipient metaconid. In one specimen  $M_2$  has a faint external trigonid cingulum, and in another this is more definite. There are two mental foramina, one beneath  $P_1$  and one beneath  $P_3$  or the anterior end of  $P_4$ . The other characters of genus and species are adequately given in the diagnosis and figures.

#### PROTHRYPTACODON FURENS Simpson

##### FIGURE 45

*Prothryptacodon furens* SIMPSON, 1935d, p. 234.

*Type*.—U.S.N.M. no. 9260, right lower jaw with  $P_4$ – $M_3$  and alveoli. Collected by A. C. Silberling.

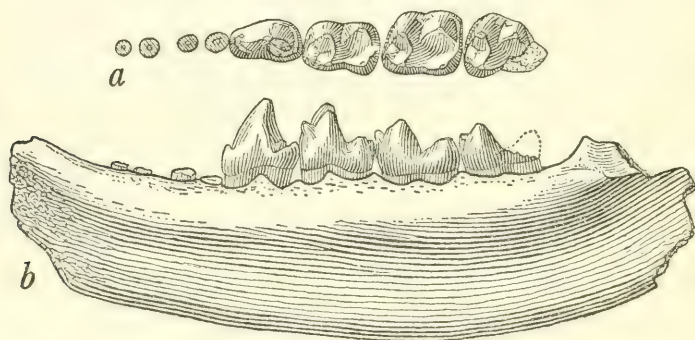
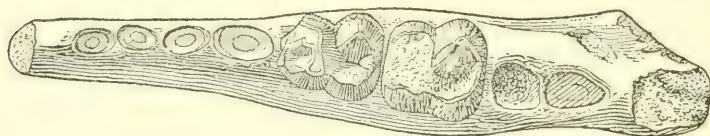
*Horizon and locality*.—Gidley Quarry (referred specimen from Silberling Quarry), Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus. Measurements in table 40.

*Remarks*.—Only two specimens are as yet known, both partial lower jaws. U.S.N.M. no. 9262 is from the Silberling Quarry.

TABLE 40.—*Individual measurements (in mm) of Prothryptacodon furens*

| Specimen               | P <sub>4</sub> |     | M <sub>1</sub> |     | M <sub>2</sub> |     | M <sub>3</sub> |     |
|------------------------|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
|                        | L              | W   | L              | W   | L              | W   | L              | W   |
| Type.....              | 4.9            | 2.7 | 5.2            | 3.7 | 5.2            | 4.2 | 5.3            | 4.0 |
| U.S.N.M. no. 9262..... |                |     |                |     | 5.1            | 4.2 |                |     |

FIGURE 45.—*Prothryptacodon furens* Simpson, U.S.N.M. no. 9260, right lower jaw: *a*, Crown view; *b*, internal view. Twice natural size.FIGURE 46.—*Chriacus pugnax* Simpson, U.S.N.M. no. 13782, right lower jaw, crown view. Twice natural size.Genus **CHRIACUS** Cope, 1883

This genus typifies the Torrejon but has been reported also in the Puerco and in the Almagre. It is improbable that a single genus had this enormous, almost unique length of distribution, and the earliest and latest forms, known only from fragments, may well prove to be distinct. The pattern is a simple and generalized one, easily confused with that of allied forms, and requiring close study and good material for its certain distinction.

The appearance of *Chriacus* in the present fauna would be expected, from its age relationships, and this genus was reported by Douglass (1908) and by me (1935d). The earlier reports, however now prove to be doubtful or erroneous. As elsewhere noted, one species hitherto referred to *Chriacus* is now placed in *Metachriacus*. The other, *C. pugnax*, is retained here, but the specimen on which it is based is so incomplete that the generic reference is not certain.



## CHRIACUS PUGNAX Simpson

## FIGURE 46

*Chriacus pugnax* SIMPSON, 1935d, p. 235.

*Type*.—U.S.N.M. no. 13782, right lower jaw with  $M_{1-2}$  and alveoli. Collected by A. C. Silberling and G. G. Simpson.

*Horizon and locality*.—Loc. 78, Fort Union, Crazy Mountain Field, Mont.

*Diagnosis*.—About the size of *C. pelvidens*, but molars wider, trigonids less elevated, talonids of  $M_{1-2}$  notably wider than trigonids.  $M_1$  length 7.1, trigonid width 4.9, talonid width 5.9.

*Remarks*.—In addition to the characters cited in the diagnosis, there is a diastema anterior to  $P_3$  in the unique specimen, but the length and significance of this cannot be established. The specimen is from one of the lowest horizons that have yet yielded mammals in this field, only 200 feet above the base of the Fort Union No. 1. This suggests comparison with *Mimotricentes angustidens*, also from a low (but not such a low) horizon, but the latter is markedly smaller and otherwise less *Chriacus*-like.

## Genus METACHRIACUS Simpson

*Metachriacus* SIMPSON, 1935d, p. 235.

*Type*.—*Metachriacus punitor* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Mont.

*Diagnosis*.—Canine and premolars about as in *Chriacus*. Molar trigonids lower than in *Chriacus* but still shearing rather than bunodont (as in *Tricentes*). Paraconids reduced and poorly distinguished, near metaconids, placed about as in *Chriacus* or slightly less internal. Accessory cuspules developing on anterior rim of trigonid, on hypoconid wings, and a slight metastylid. Upper molars with sharp cingulum around the protocone, but no protostyle. Hypocone present on  $M^1$ , rudimentary or indistinguishable on  $M^2$ , and absent on  $M^3$ .

*Remarks*.—This genus is hardly distinguishable from *Chriacus* on the basis of the premolars, which distinguish it from almost all other known genera, but the molars are of quite a different adaptive type, the lower crowns, blunter cusps, and proliferation of accessory cuspules in the lower molars representing convergences in varying degree toward *Tricentes* and toward *Claenodon*.

## METACHRIACUS PUNITOR Simpson

## FIGURES 47-49

*Metachriacus punitor* SIMPSON, 1935d, p. 235.

*Chriacus pusillus* SIMPSON, 1935d, p. 234.

*Type*.—U.S.N.M. no. 9288, left lower jaw with  $M_{1-3}$ . Collected by A. C. Silberling.

*Paratype*.—U.S.N.M. no. 9286, right lower jaw with  $P_3$ – $M_3$  ( $M_1$  and  $M_3$  broken). Collected by A. C. Silberling.

*Type of Chriacus pusillus*.—U.S.N.M. no. 9270, right lower jaw with  $P_2$ – $M_2$ . Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley and Silberling Quarries, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

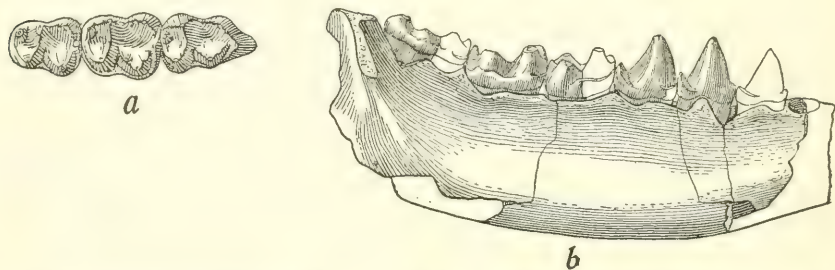


FIGURE 47.—*Metachriacus punitor* Simpson: a, U.S.N.M. no. 9288, left  $M_{1-3}$  crown view; b, U.S.N.M. no. 9286, with parts in outline from nos. 9282 and 9486, right lower jaw, external view. Twice natural size.

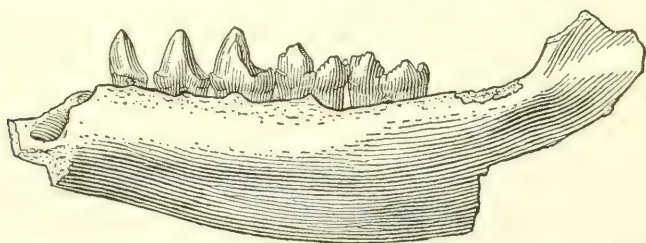


FIGURE 48.—*Metachriacus punitor* Simpson, small variation, U.S.N.M. no. 9270, right lower jaw, internal view. Twice natural size.

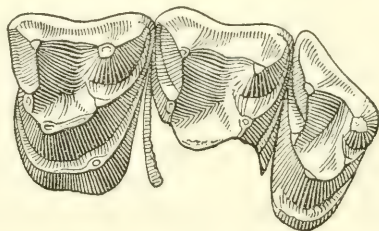


FIGURE 49.—*Metachriacus punitor* Simpson, U.S.N.M. no. 9331, left  $M_{1-3}$ , crown view. Four times natural size.

*Diagnosis*.—Heel of  $P_4$  expanded, basined, squarely truncated posteriorly. Molar crenulation moderate.  $M_{1-2}$  less wedge-shaped. Measurements given in tables 42 and 43.

*Discussion*.—My earlier publication on the two species here united was confused and incorrect. By a misinterpretation of a small worn specimen and by the acceptance of an incorrect association, I was led to place a few of these specimens in *Chriacus* and therefore I did not

properly compare them with the better materials manifestly belonging in a distinct genus, named *Metachriacus*. With the removal of the extraneous material and renewed comparison of a large number of specimens, it is clear that *Metachriacus punitor* and "*Chriacus pusillus*" both belong in *Metachriacus*. The specimens previously referred to "*Chriacus pusillus*" are smaller than those placed in *Metachriacus punitor*, and  $M_3$  is slightly more reduced. Nevertheless, with recognition that they are congeneric and in view of the fact that all are from one horizon and locality it appears that no sharp division between the small and large specimens can be made and that they are merely individual variants of one species. This is borne out by the statistical constants given below.

Of  $I_1-P_1$  only the alveoli are known. Judged from these, there were three small, subequal, closely crowded incisors, the canine was moderately enlarged and procumbent (but less so than in *Prothryptacodon*), and  $P_1$  was a small tooth implanted vertically by a single root.  $P_{2-3}$  are similar, but  $P_3$  is larger. Both are slender, 2-rooted, pointed teeth, the outer face convex, with a sharp anterior crest and the posterior and anterointernal faces excavated. There is a small barely cuspidate heel and a tiny anterior basal cuspule.  $P_4$  is considerably longer than  $P_3$  although barely higher. The anterior cuspule is more distinct and the talonid much more developed, its internal half basined. There is a high rudimentary metaconid, not well differentiated from the protoconid, closely similar to that of *Chriacus*. The lower molars are of generalized aretocyonid type except for the special characters already listed.

The symphysis is shallow, weak, and unfused, the horizontal ramus long and slender, the mental foramina beneath  $P_1$  and  $P_3$ .

Upper teeth have not been found associated with lower jaws of *Metachriacus punitor*, but there are several isolated upper teeth and jaw fragments, including representatives of the three upper molars, that are from the same level and locality, are harmonious in size and structure, and may be referred to this species with some assurance. In outline they closely resemble *Chriacus* but are distinguished by the entire absence of a protostyle and the considerably lesser development of the hypocone.

TABLE 41.—Individual measurements (in mm) of *Metachriacus punitor*

| U.S.N.M. no. | $P_2$ |     | $P_3$ |     | $P_4$   |     | $M_1$ |     | $M_2$ |     | $M_3$ |     |
|--------------|-------|-----|-------|-----|---------|-----|-------|-----|-------|-----|-------|-----|
|              | L     | W   | L     | W   | L       | W   | L     | W   | L     | W   | L     | W   |
| 9288.....    |       |     |       |     |         |     | 4.7   | 3.9 | 4.9   | 4.4 | 6.0   | 3.8 |
| 9286.....    |       |     |       |     | ca. 4.1 | 2.9 | 3.9   | 5.2 | 4.4   |     |       |     |
| 9270.....    | 2.8   | 1.6 | 3.5   | 2.0 | 4.4     | 2.6 | 4.9   | 3.7 | 5.0   | 4.3 |       |     |



Measurements of the three principal specimens and statistical constants of the whole series are given in tables 41 and 42 (see also fig. 4).

TABLE 42.—*Numerical data on lower dentition of Metachriacus punitor*

| Variate               | N | R         | M           | $\sigma$    | V         |
|-----------------------|---|-----------|-------------|-------------|-----------|
| LP <sub>1</sub> ----- | 6 | 4. 1-4. 7 | 4. 32±0. 08 | 0. 20±0. 06 | 4. 5±1. 3 |
| WP <sub>1</sub> ----- | 6 | 2. 4-3. 0 | 2. 72±0. 08 | 0. 20±0. 06 | 7. 5±2. 2 |
| LM <sub>1</sub> ----- | 5 | 4. 4-4. 9 | 4. 66±0. 07 | 0. 16±0. 05 | 3. 5±1. 1 |
| WM <sub>1</sub> ----- | 8 | 3. 5-3. 9 | 3. 71±0. 05 | 0. 16±0. 04 | 4. 1±1. 0 |
| LM <sub>2</sub> ----- | 8 | 4. 6-5. 4 | 4. 98±0. 09 | 0. 27±0. 07 | 5. 4±1. 3 |
| WM <sub>2</sub> ----- | 9 | 4. 1-4. 5 | 4. 31±0. 04 | 0. 11±0. 03 | 2. 6±0. 6 |
| LM <sub>3</sub> ----- | 6 | 5. 1-6. 1 | 5. 72±0. 14 | 0. 35±0. 10 | 6. 2±1. 8 |
| WM <sub>3</sub> ----- | 6 | 3. 6-3. 8 | 3. 68±0. 04 | 0. 09±0. 03 | 2. 4±0. 7 |

Three specimens from the Silberling Quarry, all very incomplete, are referred to this species. Each is somewhat aberrant but not consistently among the three and not beyond the established range of variation. They are not included in the figures in table 42, which are based on a pure sample from the Gidley Quarry.

#### METACHRIACUS PROVOCATOR Simpson

Figures 50-52

*Metachriacus provocator* SIMPSON, 1935d, p. 235.

*Type*.—U.S.N.M. no. 9278, left lower jaw with P<sub>4</sub>-M<sub>3</sub>. Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Type from Loc. 51, referred specimens from Locs. 81, 50, 25, 24 (all below Gidley Quarry), Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Heel of P<sub>4</sub> less expanded, little or not basined, more pointed posteriorly. Molars markedly crenulated. M<sub>1-2</sub> more wedge-shaped, i. e., talonids markedly wider than trigonids. Slightly but significantly larger than *M. punitor* in most dimensions (see table 43).

*Discussion*.—This species was originally based on three specimens (Simpson, 1935d), but since then five more, less complete, have been identified in the National Museum collection, and 10 have been collected for the American Museum, so that it is now one of the best-known species in the fauna. It does not occur in the quarries, where it is replaced by the allied but certainly distinct *M. punitor*, but occurs at the widely scattered Locs. 24, 25, 50, 51, and 81 (specimens from 25 and 81 only in the American Museum, but used in this study), all of which are somewhat below the quarries, although all in Fort Union No. 2. Both upper and lower jaws are known from each locality. It is probable that the distribution, below the quarry levels, is accidental,

that is, that *M. provocator* is not a significantly older species replaced in time by *M. punitor*, but that they may well have been really contemporaneous but living in different facies.

In addition to the characters cited in the diagnosis, the two specimens of *M. provocator* that show the alveoli of  $P_1$  had this tooth relatively more reduced than in *M. punitor*, with more definite diastemata before and behind it.

The upper molars, well known in this species, have the hypocones more definite and more projecting internally than in *M. punitor*, and  $M^3$  is less reduced and less transverse. There is also a tendency to develop a rudimentary protostyle on  $M^2$ . These characters make the upper teeth closer to *Chriacus* than are those of *M. punitor*, and the upper dentition of *M. provocator* would not perhaps in itself be separated generically from *Chriacus*, but its lower dentition shows the generic characters even more clearly than does that of *M. punitor*.

There are three lower and three upper jaws, some associated, from each of Locs. 25 and 51, three lower and one upper from Loc. 81, two lower and one upper from Loc. 50, and one lower and one upper from Loc. 24. Deviations exist, of course, between the material from different localities, but these are not consistent and are not statistically significant. The samples are too small to demonstrate racial differences, if such exist. In fact the whole combined sample does not exceed the variety usual in a homogeneous species but on the contrary shows unusually small variation, as shown by the figures in table 43 (see also fig. 4).

TABLE 43.—Numerical data on upper and lower dentition of *Metachriacus provocator*

| Variate                            | N | R         | M           | $\Sigma(d^2)$ | $\sigma$      | V         |
|------------------------------------|---|-----------|-------------|---------------|---------------|-----------|
| LP <sub>1</sub> -----              | 3 | 4. 8-5. 1 | 4. 97       | 0. 0467       |               |           |
| WP <sub>1</sub> -----              | 3 | 2. 9      | 2. 90       | 0             |               |           |
| LM <sub>1</sub> -----              | 7 | 5. 2-5. 8 | 5. 37±0. 08 | -----         | 0. 205±0. 055 | 3. 8±1. 0 |
| WM <sub>1</sub> -----              | 7 | 3. 9-4. 6 | 4. 21±0. 09 | -----         | 0. 24 ±0. 06  | 5. 7±1. 5 |
| LM <sub>2</sub> -----              | 7 | 5. 6-6. 0 | 5. 79±0. 05 | -----         | 0. 12 ±0. 03  | 2. 2±0. 6 |
| WM <sub>2</sub> -----              | 7 | 4. 6-5. 2 | 4. 91±0. 07 | -----         | 0. 19 ±0. 05  | 3. 8±1. 0 |
| LM <sub>3</sub> -----              | 4 | 6. 5-7. 0 | 6. 70       | 0. 1400       |               |           |
| WM <sub>3</sub> -----              | 5 | 4. 0-4. 3 | 4. 12       | 0. 0680       |               |           |
| LP <sub>1</sub> <sup>1</sup> ----- | 2 | 4. 6-5. 0 | 4. 80       | 0. 0800       |               |           |
| WP <sub>1</sub> <sup>1</sup> ----- | 2 | 4. 8      | 4. 80       | 0             |               |           |
| LM <sub>1</sub> <sup>1</sup> ----- | 5 | 5. 0-5. 4 | 5. 18       | 0. 1080       |               |           |
| WM <sub>1</sub> <sup>1</sup> ----- | 5 | 6. 1-6. 7 | 6. 30       | 0. 2600       |               |           |
| LM <sub>2</sub> <sup>1</sup> ----- | 7 | 5. 4-6. 1 | 5. 67±0. 09 | -----         | 0. 24 ±0. 06  | 4. 2±1. 1 |
| WM <sub>2</sub> <sup>1</sup> ----- | 7 | 7. 4-7. 9 | 7. 57±0. 07 | -----         | 0. 18 ±0. 05  | 2. 4±0. 6 |
| LM <sub>3</sub> <sup>1</sup> ----- | 4 | 4. 3-4. 8 | 4. 55       | 0. 1700       |               |           |
| WM <sub>3</sub> <sup>1</sup> ----- | 4 | 5. 8-6. 4 | 6. 15       | 0. 2700       |               |           |

In only one case does the coefficient of variation exceed 5 (this would be true also if this coefficient were calculated for all the variates).

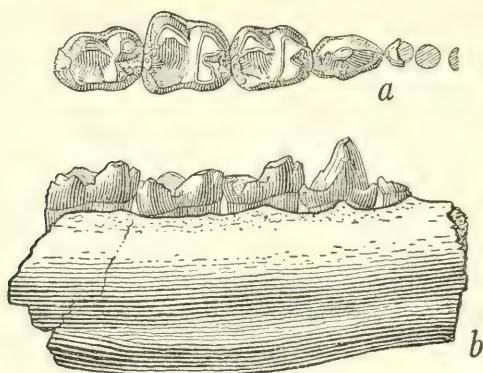


FIGURE 50.—*Metachriacus provocator* Simpson, U.S.N.M. no. 9278, left lower jaw: a, Crown view; b, internal view. Twice natural size.

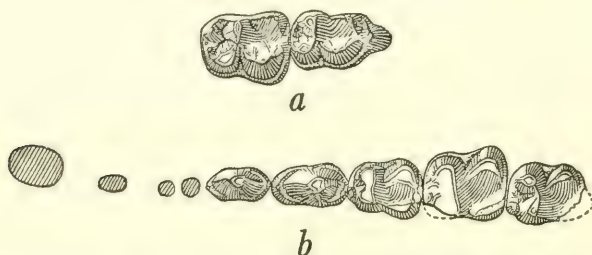


FIGURE 51.—*Metachriacus provocator* Simpson: a, U.S.N.M. no. 15126, left  $M_{2-3}$ , crown view; b, U.S.N.M. no. 9259, right lower dentition, crown view. Twice natural size.

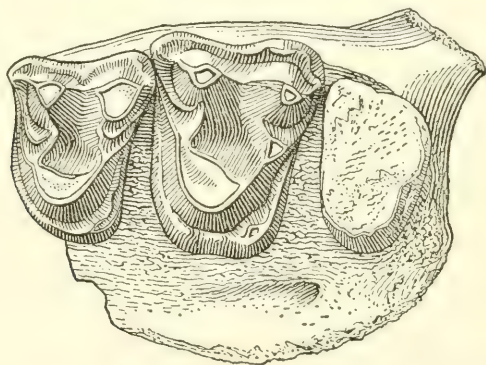


FIGURE 52.—*Metachriacus provocator* Simpson, U.S.N.M. no. 9259, left  $M_{1-2}$ , crown view. Four times natural size.

The difference from *M. punitor* is so obvious that its significance requires no proof. In every case the deviation between the means is significant, and in the available samples the observed ranges overlap, barely, only for the widths of  $P_4$  and  $M_1$ .



The individual dimensions of the type lower jaw are as follows: Length  $P_4$ , 5.0; width  $P_4$ , 2.9; length  $M_1$ , 5.5; width  $M_1$ , 4.1; length  $M_2$ , 5.7; width  $M_2$ , 5.2; length  $M_3$ , 6.5; width  $M_3$ , 4.0.

#### Genus SPANOXYODON Simpson

*Spanoxyodon* SIMPSON, 1935d, p. 236.

*Type*.—*Spanoxyodon latrunculus* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.— $P_{1-2}$  absent and long diastema between canine and  $P_3$ .  $P_{3-4}$  much as in *Chriacus*, but  $P_4$  with metaconid larger, higher, and more distinct.  $M_{1-2}$  about as in *Chriacus* or with trigonids slightly lower and paraconids slightly less internal.

*Remarks*.—Only one specimen referable to this genus is yet known, and its characters are adequately summed up in the diagnosis.

#### SPANOXYODON LATRUNCULUS Simpson

##### FIGURE 53

*Spanoxyodon latrunculus* SIMPSON, 1935d, p. 236.

*Type*.—U.S.N.M. no. 9287, left lower jaw with canine alveolus and  $P_3$ – $M_2$ . Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus. Measurements of type as follows: Length  $P_3$ , 3.8; width  $P_3$ , 2.3; length  $P_4$ , 5.0; width  $P_4$ , 2.8; length  $M_1$ , 5.2; width  $M_1$ , 3.9; length  $M_2$ , 5.8; width  $M_2$ , 4.5.

#### MIMOTRICENTES,<sup>89</sup> new genus

*Type*.—*Tricentes latidens* Gidley.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Adaptively and structurally closely similar to *Tricentes*, but  $P_1$  present, no marked diastema, and molar paraconids higher on crown and internal, not median, in position.

*Discussion*.—In my preliminary paper I left the type of this genus in *Tricentes*, where Dr. Gidley had placed it. On further study, however, I am forced to erect a new genus for it. The resemblance to *Tricentes* is close, but in the latter  $P_1$  is apparently invariably absent (the name *Tricentes* refers to the presence of only three premolars, striking in this primitive fauna), and the paraconids of  $M_{2-3}$  are quite different. The former might be only a primitive character and not surely of generic rank if unaccompanied by other differences. The character of the paraconid, however, as reduced as in *Tricentes* but in a different way, removes this form from the *Tricentes* lineage and may even mean that the relationship is not closer to that genus than

<sup>89</sup> Μῑμος, an imitator + *Tricentes*.

to other primitive arctocyonids and that the resemblance is purely convergent, aside from the fact that both have the stereotyped pattern of all these ancient forms.

The canine, preserved in the type, has a large root and is curved in a pronounced arc. The crown is unusually erect, as it is also in *Tricentes*.  $P_1$  is known only by its alveolus, which is single and rather large. The premolars very closely resemble those of *Tricentes*, except

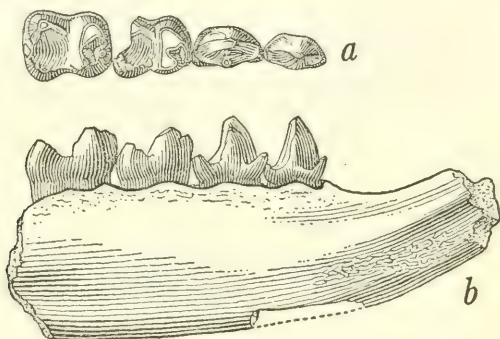


FIGURE 53.—*Spanoxyodon latrunculus* Simpson, U.S.N.M. no. 9287, left lower jaw: *a*, Crown view; *b*, internal view. Twice natural size.

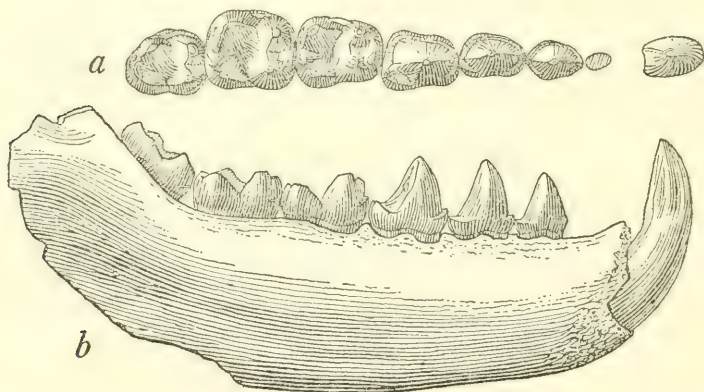


FIGURE 54.—*Mimotricentes latidens* (Gidley), U.S.N.M. no. 9269, left lower jaw: *a*, Crown view; *b*, internal view. Twice natural size.

that the heel of  $P_4$  is more expanded transversely and its posterior border is more nearly a straight transverse line—a distinction probably not generic, as it is closely similar to that between *Metachriacus punitor* and *M. provocator*. The molars are even flatter and broader than in *Tricentes* but otherwise closely resemble those of that genus except for the difference in the paraconids. Upper teeth are known only in one specimen, mentioned below.

## MIMOTRICENTES LATIDENS (Gidley)

## FIGURE 54

*Tricentes latidens* GIDLEY, Simpson, 1935d, p. 236.

*Type*.—U.S.N.M. no. 9269, left lower jaw with canine and  $P_2$ - $M_3$ . Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Length: width ratio (type only):  $M_2$  1.09,  $M_3$  1.30. Measurements given in table 44. Paraconids vestigial and trigonids short.

*Discussion*.—This species is known principally from two good specimens from the Gidley Quarry, the type and U.S.N.M. no. 9276, a right lower jaw with  $P_2$ - $M_2$  ( $M_2$  broken), confirming but not adding to knowledge derived from the type. There are two other specimens from the Gidley Quarry, probably of this species but of no value, and two, also very fragmentary, from the Silberling Quarry. One of the latter, U.S.N.M. no. 9672, with  $P_4$  and  $M_1$ , is smaller and less robust than the type, with the paraconid of  $M_1$  more distinct, but it might be a variant of this species.

The only known upper teeth of this genus, and probably but not surely this species, are  $M^{2-3}$  from Loc. 81, in the American Museum collection. Like the lower molars, they closely resemble those of *Tricentes*, the only clear difference, and this of doubtful value, being that the internal cingulum does not circle the protocone and that on  $M^2$  the external cingulum does not cross the paracone.

TABLE 44.—Measurements (in mm) of the two principal Gidley Quarry specimens of *Mimotricentes latidens*

| U. S. N. M. no. | $P_2$ |     | $P_3$ |     | $P_4$ |     | $M_1$ |     | $M_2$ |     | $M_3$ |     |
|-----------------|-------|-----|-------|-----|-------|-----|-------|-----|-------|-----|-------|-----|
|                 | L     | W   | L     | W   | L     | W   | L     | W   | L     | W   | L     | W   |
| 9269.....       | 3.6   | 2.8 | 4.6   | 3.3 | 5.4   | 4.0 | 5.5   | 4.7 | 6.0   | 5.5 | 6.1   | 4.7 |
| 9276.....       | 3.8   | 2.8 | 4.5   | 3.3 | 5.3   | 3.8 | 5.7   | 4.7 |       |     |       |     |

MIMOTRICENTES ANGUSTIDENS,<sup>90</sup> new species

## FIGURE 55

*Type*.—U.S.N.M. no. 9277, left lower jaw with  $P_4$ - $M_2$ . Collected by A. C. Silberling.

*Horizon and locality*.—Type from Silberling Quarry. Referred specimens, not identified with complete certainty, from Locs. 51 and 73. Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

<sup>90</sup> *Angustus*, narrow+dens, tooth.



*Diagnosis*.—Very slightly smaller than *M. latidens*.  $P_4$  relatively smaller, slender, and with paraconid much stronger. Molars relatively narrower. Length: width ratio of  $M_2$  (of type) 1.24. Paraconids less reduced and trigonids less compressed than in *M. latidens*, trigonids about equal to talonids in size.

*Discussion*.—The difference in size is slight and may not be significant, but the differences in structure and proportions are marked and sharply distinguish this from *M. latidens*. The type has another distinction, not cited in the diagnosis, in the fact that the talonid of  $M_2$  is definitely narrower than the trigonid, while in *M. latidens* it is of equal width or slightly wider than the trigonid. There are, however, two isolated  $M_2$ 's from Loc. 50 that closely resemble *M. angustidens* but that have the talonid in one equal to the trigonid and in the other slightly wider. At present it seems more probable that this is a variable character in the species than that these teeth represent a third species.

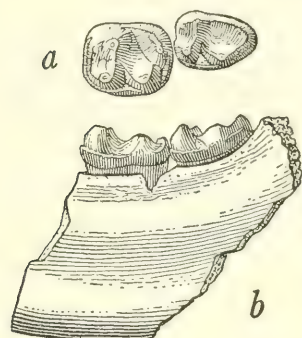


FIGURE 55.—*Mimotricentes angustidens*, new genus and species, Princeton Univ. no. 13758, left lower jaw, a, Crown view; b, internal view. Twice natural size.

Princeton no. 13758 is a left lower jaw with  $M_{2-3}$ , from Loc. 73, especially interesting because it is from the Fort Union No. 1, where fossils are very rare and because it is, as far as I know, the only fossil mammal ever found in sandstone in this field. Its  $M_2$  agrees very closely with the

type of *M. angustidens* except that the talonid is as wide as the trigonid.  $M_3$  differs from that of *M. latidens* in the same way as does  $M_2$ , being relatively narrower, with stronger paraconid and longer trigonid.

The dimensions of the four specimens mentioned are given in table 45.

TABLE 45.—*Individual measurements (in mm) of lower dentition of Mimotricentes angustidens*

| Specimen                 | $P_4$ |     | $M_1$ |     | $M_2$ |     | $M_3$ |     |
|--------------------------|-------|-----|-------|-----|-------|-----|-------|-----|
|                          | L     | W   | L     | W   | L     | W   | L     | W   |
| U.S.N.M. no. 9277.....   | 4.4   | 3.0 | 4.8   | 3.6 | 5.6   | 4.5 |       |     |
| U.S.N.M. no. 9706.....   |       |     |       |     | 5.6   | 4.6 |       |     |
| U.S.N.M. no. 9695.....   |       |     |       |     | 5.6   | 4.5 |       |     |
| Princeton no. 13758..... |       |     |       |     | 5.7   | 4.6 | 5.5   | 3.6 |

## ?MIMOTRICENTES species

U.S.N.M. no. 6178 is a left  $M_2$  from Loc. 9, at a low level in the formation. It apparently belongs in this or a closely allied genus. Its dimensions, 6.2 by 5.2 mm, are perhaps not significantly different from those of *M. latidens*, although it is relatively somewhat narrower. The trigonid is distinctly longer than in the type of the genus and about equal to the talonid in size, not distinctly smaller as in the type. Although inadequate for identification, the occurrence merits mention in view of the horizon represented.

## Family MIACIDAE Cope, 1880

The known history of the Miacidae is anomalous and emphasizes the inadequacy of some of our knowledge of details in this early epoch and the probably erroneous character of some negative conclusions regarding it. The miacids (so carefully and fully defined by Matthew in many works that diagnosis here is unnecessary) are a specialized group, for in them the carnassial shearing teeth are very well developed, despite their absence in all other known Lower and Middle Paleocene mammals. Furthermore, they are an adaptive and potent group, for their carnassials are  $M_1$  and  $P^4$ , as in the Carnivora (*vera*) or Fissipedia and there is every reason to believe that they are, in a broad sense, ancestral to all the latter. The appearance of this apparently modernized group in a fauna otherwise almost wholly archaic is extraordinary.

The known distribution within the family is also noteworthy. The first genera to appear, and the only ones known before the true Eocene, are not the most primitive and generalized and are not ancestral, even structurally, to the majority of later types. All have lost  $M^3_3$ , unquestionably present in the ancestry. Even aside from the fact that these teeth are present in most later miacids, they are almost universally present in Middle Paleocene mammals of other families.

This anomalous history must involve, first, rapid progressive evolution of the group generally, the Miacidae, which is not surprising in view of later history, which shows this general type to be probably the most plastic and adaptive of all mammals. Second, it must involve the early, minor differentiation of a special line, the Viverravinae, which entered the regions known to us paleontologically at about the beginning of the Middle Paleocene, while the more varied adaptive Miacinae were confined, until the great Eocene invasion, to some facies or region still unknown to us.

In speaking of the Miacidae as specialized, it is important to emphasize the relative value of the words. They are specialized in comparison with the extraordinarily archaic contemporaneous Arctocyonidae, which are not far from being generalized primitive placentals, but in comparison with the other carnivores, specifically with the

fissipedes, they are extremely primitive, much more so than any Tertiary dogs or other true fissipedes. The anomaly is thus not so striking as might appear at first sight. Furthermore, within the family the Paleocene forms are distinctly more primitive than Eocene Viverravinae and are certainly not ancestral to the Miacinae, so that comparison with the latter is misleading. On a small scale, within the family, the Viverravinae are a miniature "archaic" radiation of Miacidae and the Miacinae a later "progressive" radiation, much as, on a far grander scale, the peculiarly specialized peripitychids are an archaic radiation and the basically more primitive hyracotheres are a progressive radiation among the ungulate cohort.

There are two distinctive genera of miacids in this fauna, *Didymictis*, evidently an abundant form with several species and long known from the distant Torrejon (as well as from numerous later horizons), and *Ictidopappus*, a rarer type known from only two specimens in this fauna and as yet unknown elsewhere.

Subfamily VIVERRAVINAE Matthew, 1909 (Viverravidae Wortman and Matthew, 1899)

*Viverravus*, *Didymictis*, and *Ictidopappus* evidently form a closely related group characterized, among other features, by the prominent anteroexternal cuspule of  $P^1$ , the elongate oval outline of  $M^2$ , and the absence of  $M^3$  (Matthew, 1915). For this group the name Viverravinae is available, contrasting with the typical miacids, the Miacinae. As mentioned below, *Didymictis* may be a compound genus, but if so its components are very closely related. *Viverravus*, also, is a somewhat doubtfully bounded genus. Its earlier, lower Eocene species are very close to *Didymictis*, while some of its later, middle Eocene species, perhaps including the genotype, are so markedly advanced over the early forms that they might not ordinarily be placed in the same genus. This point is not here apropos, but *Viverravus* is of some present interest because of the possibility of special relationship to *Ictidopappus*.

*Viverravus* and *Didymictis* were separated by Matthew (1915) on the basis of the crested heels of  $M_{1-2}$  in the former, basined in the latter. In fact the early species of *Viverravus* (e. g., *V. acutus*, *V. politus*, and even the slightly later *V. dawkinsianus*) do have basined talonids, although they are obviously becoming crested by emphasis of the hypoconid and marked reduction of the entoconid. In *Ictidopappus* the talonids are quite as basined as in *Didymictis*, a condition doubtless ancestral for *Viverravus* also but partly or completely lost in species definitely referable to that genus. Aside from the difference in the heel, relatively slight at the beginning of the Eocene, the early species of *Viverravus* also differ from *Didymictis* in the longer, lower trigonid of  $M_1$ , which is a striking resemblance to *Ictidopappus*.



Were it not for the unusual proportions and simple structure of  $P_4$ , *Ictidopappus* would make an ideal ancestor for *Viverravus*. Some species of the latter, e. g., *V. acutus*, have  $P_4$  small and simple, but much more trenchant than in *Ictidopappus*, strongly compressed laterally, the posterior cusps well developed, and all cusps in a straight line, not subtriangular. The *Ictidopappus*  $P_4$  might be ancestral to this, but there is no good evidence that it was, and *Viverravus* may after all be an offshoot of *Didymictis* in which the trenchant  $P_4$  was already highly developed in the Middle Paleocene.

#### Genus DIDYMICTIS Cope, 1875

This exceptionally long-lived genus is recorded from all levels from the Torrejon to the end of the lower Eocene. During this period there is not only definite evolutionary advance but also evidence of the presence of several different phyla. It is quite possible that one or more of these can be and should be separated generically, but the criteria for doing so are poor at present. A useful step was Matthew's (especially 1915) revalidation of *Viverravus*, which was long confused with *Didymictis* or considered a synonym. Now Matthew (Pale. Mem.) has further separated the sole Torrejon species, *D. haydenianus*, and placed it in a new subgenus, *Didymictis* (*Protictis*), with the suggestion that this may prove to be of generic rank.

The most abundant species in the present collection, *D. microlestes*, introduces some difficulty in this arrangement. In its more important morphological characters it compares with the types of *Didymictis* (*Protictis*) and of *Didymictis* (*Didymictis*) as shown in table 46.

TABLE 46.—Comparison of dentition characters of three species of *Didymictis*

| Species                             | $P^2$                       | Protocone of $M^1$                   | Proportions of $M^1-M^2$             |
|-------------------------------------|-----------------------------|--------------------------------------|--------------------------------------|
| <i>D. (Protictis) haydenianus</i> . | With rudimentary protocone. | High, angulate, posterior wing weak. | Strongly transverse, $M^1$ reduced.  |
| <i>D. microlestes</i> -----         | Intermediate.....           | As in <i>D. protenus</i> -----       | As in <i>D. protenus</i> .           |
| <i>D. (Didymictis) protenus</i> .   | Compressed, no protocone.   | Broader, wings equal.....            | Less transverse, $M^2$ less reduced. |

| Species                             | $P_3$                                                                                       | $P_4$                                                                                                    | $M_2$                                                             |
|-------------------------------------|---------------------------------------------------------------------------------------------|----------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------|
| <i>D. (Protictis) haydenianus</i> . | With very minute anterior cuspule, heel crested without distinct cusp.                      | With distinct, nonshearing anterior cusp, 2 talonid cuspules, small basin.                               | With trigonid somewhat elevated and shearing, heel reduced.       |
| <i>D. microlestes</i> -----         | With relatively large anterior cusp, heel with small basin and crest with rudimentary cusp. | With anterior cuspule large and shearing, 1 talonid cuspule, small basin.                                | Trigonid comparable to <i>D. haydenianus</i> , heel less reduced. |
| <i>D. (Didymictis) protenus</i> .   | With minute anterior and large posterior accessory cusp, no basin.                          | With anterior cuspule very small, nonshearing, 1 talonid cuspule, basin very poorly developed or absent. | With trigonid low, tubercular, heel not reduced.                  |

The upper teeth, although much smaller and lighter in construction, resemble *D. protenus* rather than *D. haydenianus*. These are probably primitive characters, and *D. haydenianus* is slightly aberrant. The development of  $P_{3-4}$  is also somewhat closer to *D. protenus*, and it is not clear that this is wholly in primitive characters. The presence of only one talonid cusp on  $P_4$  may be, but it is unlikely that the more cuspidate  $P_3$  is primitive. The development of relatively large and shearing anterior cuspules on these teeth is different from either *D. haydenianus* or *D. protenus* and seems to be a specialization.  $M_2$  is perhaps merely primitive with respect to either of the other two species.

It is possible that *D. microlestes* stands nearer the *D. protenus* ancestry than does *D. haydenianus*, in which case the subgeneric separation might well be maintained, and *D. microlestes* would belong to the typical subgenus. The evidence for this is not very good, however, and for the present it seems best not to attempt a subdivision of the genus.

There is another *Didymictis*-like species in the fauna, *D. tenuis*, of very diminutive size. At present it is known from a single specimen, and, as noted below, there is some doubt as to the characters of  $P_4$ . If they were confirmed the species could hardly be placed in *Didymictis*, but knowledge is now so imperfect that it seems best to leave it here until further evidence is at hand. Table 47 gives an idea of the very considerable differences in the length of  $M_1$  among the three Middle Paleocene species referred to *Didymictis*:

TABLE 47.—Length of  $M_1$  in three species of *Didymictis*

| Species                              | N | R       | M    |
|--------------------------------------|---|---------|------|
| <i>D. haydenianus</i> —Torrejon..... | 6 | 7.5–8.0 | 7.72 |
| <i>D. microlestes</i> .....          | 8 | 4.3–5.1 | 4.66 |
| <i>D. tenuis</i> .....               | 1 | -----   | 2.9  |

There are also a few specimens too imperfect for exact identification that are comparable in size to *D. haydenianus* and cannot at present be distinguished from that species.

## DIDYMICTIS MICROLESTES Simpson

Figures 56, 57

*Didymictis microlestes* SIMPSON, 1935d, p. 238.

*Type*.—U.S.N.M. no. 9301, left lower jaw with  $P_4$ – $M_2$ . Collected by Dr. J. W. Gidley.

*Horizon and locality.*—Gidley Quarry (one referred specimen from Silberling Quarry), Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—Much smaller than *D. haydenianus* or any known later species (see measurements below).  $P_3$  similar to  $P_4$ , but cuspules less well developed.  $P_4$  with large anterior cuspule, developed into a small shearing blade, talonid relatively broad and less rounded than in other species, with one main cusp.  $M_2$  with slightly elevated and shearing trigonid, talonid reduced.

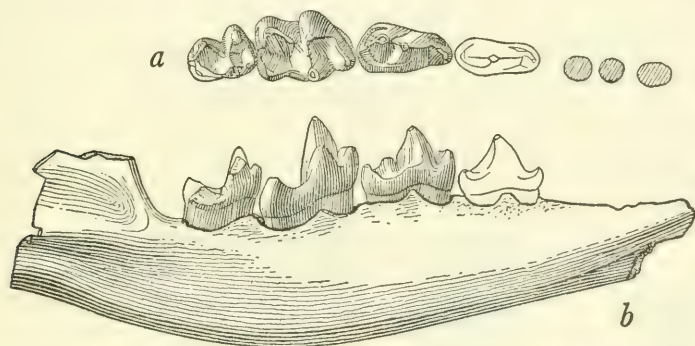


FIGURE 56.—*Didymictis microlestes* Simpson, U.S.N.M. no. 9301, with parts in outline supplied from U.S.N.M. nos. 6146 and 9306, left lower jaw; *a*, Crown view; *b*, internal view. Three times natural size.



FIGURE 57.—*Didymictis microlestes* Simpson, U.S.N.M. no. 9299, with part in outline supplied from no. 6147, left  $P^1$ – $M^1$ , crown view. As preserved,  $P^1$  is reversed (or rotated  $180^\circ$ ) from the position shown in the drawing, but this is believed to be accidental. Three times natural size.

*Discussion.*—The morphological characters of this elegant little species have been fully brought out in the comparison and diagnosis above. The principal available numerical data on the lower dentition are given in table 48.

TABLE 48.—Numerical data on lower dentition of *Didymictis microlestes*

| Variate      | N | R       | M               | $\sigma$                 | V             |
|--------------|---|---------|-----------------|--------------------------|---------------|
| $LP_4$ ----- | 7 | 4.1–5.0 | $4.49 \pm 0.11$ | $0.28 \pm 0.07$          | $6.2 \pm 1.7$ |
| $WP_4$ ----- | 7 | 2.0–2.5 | $2.17 \pm 0.06$ | $0.17 \pm 0.04$          | $7.7 \pm 2.0$ |
| $LM_1$ ----- | 8 | 4.3–5.1 | $4.66 \pm 0.09$ | $0.26 \pm 0.06$          | $5.6 \pm 1.4$ |
| $WM_1$ ----- | 8 | 2.9–3.2 | $3.08 \pm 0.03$ | $0.097 \pm 0.024$        | $3.1 \pm 0.8$ |
| $LM_1$ ----- | 4 | 3.4–3.8 | 3.65            | $[\Sigma(d^2) = 0.0900]$ |               |
| $WM_1$ ----- | 4 | 2.2–2.3 | 2.25            | $[\Sigma(d^2) = 0.0100]$ |               |



The type happens to be an unusually small specimen. It measures: Length  $P_4$ , 4.2; width  $P_4$ , 2.1; length  $M_1$ , 4.3; width  $M_1$ , 3.2; length  $M_2$ , 3.4; width  $M_2$ , 2.2.

Only two upper jaws and an isolated carnassial are at hand, measurements of which are given in table 49.

TABLE 49.—Individual measurements (in mm) of upper dentition of *Didymictis microlestes*

| U.S.N.M. no. | $P_4$ |     | $M_1$ |     | $M_2$ |     |
|--------------|-------|-----|-------|-----|-------|-----|
|              | L     | W   | L     | W   | L     | W   |
| 9299-----    |       | 3.9 | 4.2   | 5.4 | 2.4   | 4.0 |
| 9300-----    | 4.9   | 3.8 | 4.3   | 5.1 | 2.5   | 3.9 |
| 6147-----    | 5.1   | 4.1 |       |     |       |     |

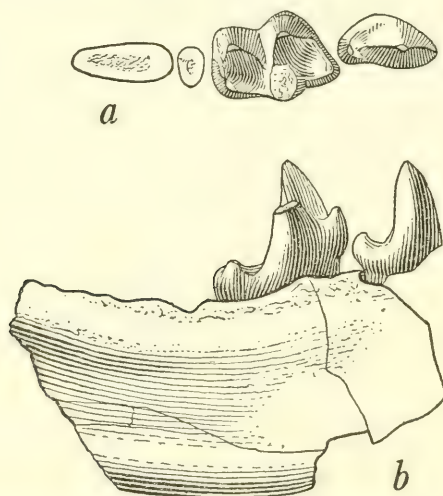


FIGURE 58.—*Didymictis tenuis* Simpson, U.S.N.M. no. 9297, left lower jaw: a, Crown view; b, internal view.  $P_4$  is broken, and it may not be correctly placed. Six times natural size.

#### DIDYMICTIS TENUIS Simpson

##### FIGURE 58

*Didymictis tenuis* SIMPSON, 1935d, p. 238.

*Type*.—U.S.N.M. no. 9297, part of left lower jaw with  $M_1$  and broken  $P_4$ . Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Much smaller than any known comparable miacid.  $M_1$  with very elevated trigonid, hypoconid and entoconid about equally high and distinct.  $M_1$  length 2.9, width 1.8.

*Remarks.*—As the specimen is preserved there is a small tooth anterior to  $M_1$  that has been cemented to the specimen without any clear or certain contact. Knowing the care with which Dr. Gidley worked, I have no doubt that this tooth was found with the specimen, but not knowing his exact evidence of association I am not certain that it is in fact  $P_4$  of this individual. It is, furthermore, somewhat incomplete. It appears to be a very small and simple tooth with a short, high, conical main cusp and a single conical posterior cusp. If these are its true characters, it is very much unlike  $P_4$  in any species certainly referred to *Didymictis*, but this is too uncertain to draw any conclusion, and the lower carnassial is sufficiently *Didymictis*-like to leave the species in that genus at least until better material is found.

**DIDYMICTIS HAYDENIANUS Cope, 1882**

FIGURE 59

U.S.N.M. nos. 6143 and 6145, each including an upper  $P^4$ , represent a species inseparable from *Didymictis haydenianus*. Their most reliable dimension, the (oblique) length of the straight shearing edge, is 10.7 and 9.7 mm, respectively. In Torrejon specimens referable to *D. haydenianus* this dimension is 9.2–11.3 mm. No constant morphological difference is seen. The material is inadequate to establish definitely that the Fort Union form is exactly the same as that from the Torrejon, but obviously it is not separable.

In the American Museum collection there is a specimen from Loc. 81 with broken  $P^4$  and  $M^1$ . The oblique length of the shearing crest cannot be measured exactly, but it was about 11.2 mm near the known upper limit for *D. haydenianus*. The specimen is more robust than the two mentioned above and might be a large variant of the same form or a different subspecies or species.

There is also a fragment of a  $P_4$ , including the heel, U.S.N.M. no. 9930, from Loc. 51, that has the size and cusp structure of *D. haydenianus*, quite unlike *D. microlestes*.

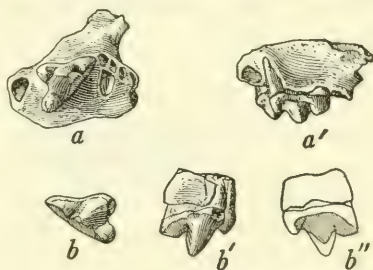


FIGURE 59.—*Didymictis haydenianus* Cope, referred specimens from the Lebo: *a*, U.S.N.M. no. 6145, left upper jaw with carnassial, crown view; *a'*, same, external view; *b*, U.S.N.M. no. 6143, right upper carnassial, crown view; *b'*, same, anteroexternal view; *b''*, same, postero-internal view in outline with wear surface cross-hatched. Natural size.

**Genus ICTIDOPAPPUS Simpson**

*Ictidopappus* SIMPSON, 1935d, p. 237.

*Type.*—*Ictidopappus mustelinus* Simpson.

*Distribution.*—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.—Differing from *Didymictis* in the relatively smaller and much simpler  $P_{3-4}$  and relatively lower and longer trigonid of  $M_1$ , from *Viverravus* in the wider and more triangular  $P_4$  and more definitely basined talonids, and from other known miacids in the absence of  $M_3$ .

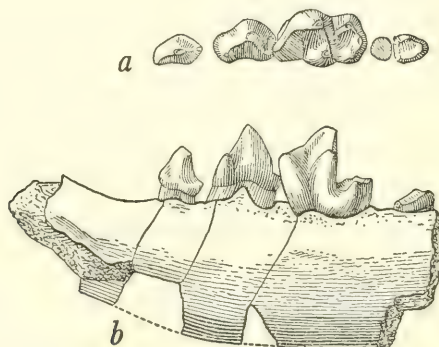


FIGURE 60.—*Ictidopappus mustelinus* Simpson, U.S.N.M. no. 9296, right lower jaw: *a*, Crown view; *b*, internal view. Three times natural size.

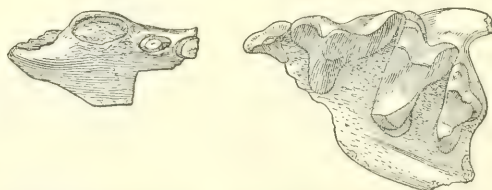


FIGURE 61.—*Ictidopappus mustelinus* Simpson, U.S.N.M. no. 9295, left upper jaw, in two fragments but associated, crown view. Three times natural size.

#### ICTIDOPAPPUS MUSTELINUS Simpson

FIGURES 60, 61

*Ictidopappus mustelinus* SIMPSON, 1935d, p. 237.

*Type*.—U.S.N.M. no. 9296, right lower jaw with  $P_3$ – $M_1$  and talonid  $M_2$ . Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus. Measurements below.

*Discussion*.—From the alveoli the canine was a large procumbent tooth and was followed by a diastema.  $P_1$  may have been absent and  $P_2$  1-rooted, but this is not certain.  $P_3$  is a very small and simple tooth consisting of a somewhat compressed main cusp followed by a slight unbasined heel.  $P_4$  is shorter than  $M_1$  but nearly as high and is sub-



triangular. There is a small anterointernal cusp, resembling a rudimentary paraconid rather than the anterior basal cuspule of *Didymictis*, and there is a very slight and uncertain indication of a rudimentary basal metaconid. The talonid is very short and wide and vaguely cusped. There are no other cuspules or cingula.

M<sub>1</sub> has a large but, in comparison with *Didymictis*, low trigonid elongate anteroposteriorly. The talonid is very small, with distinct but not prominent hypoconid, hypoconulid, and entoconid developed on its raised rim. Its well-developed basin opens internally, between entoconid and metaconid base. M<sub>2</sub> was evidently much reduced. The talonid is small but is elongate and basined, with the three cusps poorly differentiated. The specimen is broken immediately posterior to this, but from the shape of the talonid of M<sub>2</sub> it cannot have been followed by another tooth. Dimensions are as follows: Length P<sub>3</sub>, 2.0; width P<sub>3</sub>, 1.4; length P<sub>4</sub>, 2.9; width P<sub>4</sub>, 1.9; length M<sub>1</sub>, 3.8; width M<sub>1</sub>, 2.3.

There is a specimen, U.S.N.M. no. 9295, a left maxilla with P<sup>1</sup>, P<sup>3</sup>-M<sup>2</sup>, and the alveolus of the canine, that is probably the upper jaw of *Ictidopappus mustelinus*. Its size is exactly right for occlusion with the type, it has P<sup>3</sup> much smaller than in *Didymictis*, harmonious with the smaller P<sub>4</sub> of the type, and it has M<sup>1-2</sup> markedly shorter than in *Didymictis*, harmonious with the shorter M<sub>2</sub> and heel of M<sub>1</sub> of the type. The only feature suggesting distinction is the embrasure between P<sup>4</sup> and M<sup>1</sup>, the outer angle of which is much more acute than the outer angle of the trigonid of M<sub>1</sub>, which fits into it. This, however, does not prevent normal occlusion, as it might at first sight appear to do. In *Didymictis*, also, the embrasure angle is more acute than the occluding trigonid angle. Occlusion is not strictly orthal but is oblique, in part ectal (in fact nearly analogous to the triconodont occlusion but, unlike triconodonts, interlocking). At the close of the bite the external trigonid angle is internal to the embrasure angle, and the trigonid fits into the wider internal part of the embrasure and does not coincide with it. It cannot be proved that this upper jaw is of *Ictidopappus*, but it is highly probable, and it should not be assumed to be distinct.

The generic distinction of the upper jaw is very marked. The canine was relatively large, its alveolar wall swollen, much as in the most advanced and quite unlike the primitive species of *Didymictis*. P<sup>1</sup> is present and a small simple tooth probably with two roots but with alveolar mouths confluent. (P<sup>2</sup> is represented by one root, the specimen being broken here.) P<sup>3</sup> is much smaller than in *Didymictis*. Its ectoloph is similar in form. The pronounced inner spur, worn but probably not cuspidate, is median and has a separate and strongly divergent root. The ectoloph of P<sup>4</sup> is also similar to *Didymictis* but has a more decided notch in the external contour and is without a cingulum. The protocone spur is slenderer, perhaps less definitely

cusped (worn) and projects almost directly internally, not at all forward, in marked distinction from *Didymictis*.

M<sup>1-2</sup> have the same cusp structure as in all miacids, but are highly peculiar in proportions, being very short and wide, markedly triangular, not at all rounded, with sharply emarginate external borders. These characters are more nearly approached by *Viverravus* than by *Didymictis* but sharply distinguish *Ictidopappus* from any other miacid.

Measurements of this specimen are as follows: Length P<sup>3</sup>, 2.6; length P<sup>4</sup>, 4.8; width P<sup>4</sup>, 3.7; length M<sup>1</sup>, 3.2; width M<sup>1</sup>, 5.2; length M<sup>2</sup>, 2.0; width M<sup>2</sup>, 3.7.

### Family MESONYCHIDAE Cope, 1875

This family, so widespread elsewhere in the Middle Paleocene and on into the Eocene, is represented in the present fauna only by two broken teeth.

#### Genus DISSACUS Cope, 1881

##### DISSACUS, species undetermined

U.S.N.M. no. 9692 from the Gidley Quarry is the base of a tooth with the heel preserved. It agrees in size with M<sub>2</sub> of *Dissacus navajovius*, of the Torrejon, but differs in having a very vestigial basin internal to the heel crest. Another specimen, from the Gidley Quarry, is perhaps M<sub>1</sub>, lacking the anterior portion. The metaconid is very small and is relatively anterior, as in some species of *Dissacus*, but the heel is relatively shorter than in other specimens of that genus known to me. It is clear that these fragments are mesonychid, and there is nothing to distinguish them certainly from *Dissacus*, but they are not really identifiable.

### Order CONDYLARTHRA Cope, 1881

As with most of the major groups here considered, Matthew has thoroughly reviewed the taxonomic history of the order Condylarthra. Since, however, I propose a marked change in the current arrangement of the order, an outline of this history must now be given. Cope proposed the name Condylarthra (then supposed to be a suborder of Perissodactyla) in 1881, basing it on the Phenacodontidae and principally on *Phenacodus* but with *Periptychus* ("*Catathlaeus*"), *Mioclaenus*, and *Tetraclaenodon* ("*Protogonia*") probably and *Anisonchus* possibly included. Subsequently (1882-1884) the family Periptychidae was distinguished, but retained in the Condylarthra, the family Meniscotheriidae was added, and *Mioclaenus* was excluded, being considered first an artiodactyl, then a creodont. On the latter point, Scott (1892) showed that many species placed in *Mioclaenus* by Cope were

generically distinct and were indeed creodonts, while *Mioclaenus*, *sensu stricto*, might be a condylarth, in which case it would form a very distinct family.

In 1895 Osborn and Earle followed Scott's suggestion and defined the Mioclaenidae as a family of condylarths. They retained the three condylarth families of Cope, Periptychidae, Phenacodontidae, and Meniscotheriidae. They divided the Periptychidae into Anisonchinae and Periptychinae and stressed the resemblance of the former to the Mioclaenidae. They also noted that the Periptychidae had resemblance to the Amblypoda and suggested the possibility of their belonging there, but left them in the Condylarthra. In one of his last papers, in 1897, Cope adopted this suggestion and associated the Periptychidae with the Pantolambdidae in the division Taligrada of the Amblypoda. In the same year, but with Cope's paper before him, Matthew rejected this transfer and adduced new evidence and reasons for retaining the Condylarthra as a broad group including Periptychidae, Phenacodontidae, Mioclaenidae, and Meniscotheriidae. In 1898 Osborn adopted Cope's arrangement of the Amblypoda, including the Periptychidae in the Taligrada and hence excluding it from the Condylarthra.<sup>91</sup> He seems subsequently to have adhered constantly to the conception of the Condylarthra as including only the Phenacodontidae, Mioclaenidae, and Meniscotheriidae, and this authoritative view has since been the most widespread. Matthew continued for a time to include the Periptychidae but after about 1914 agreed with Cope and Osborn in placing that group in the Amblypoda.

The relationship of the hyopsodonts to this order was not established until relatively recently, and even now the conclusive evidence for it does not appear to be widely known. From the time of its discovery by Leidy in 1870 until 1903 *Hyopsodus* was universally considered to be allied to *Notharctus*, *Pelycodus*, or similar genera. It was therefore generally considered to be a primate, occasionally an insectivore, but in these instances largely on the evidence of supposed allies, which are in fact primates. In 1903 Wortman definitely distinguished *Hyopsodus* from the early lemuroids and referred it, in the family Hyopsodontidae (defined but incorrectly delimited by Schlosser in 1887 and recognized under an invalid name by Marsh in 1875), to the Insectivora, on its own characters, not those of lemuroid supposed allies. In 1909 Matthew thoroughly reviewed the Bridger hyopsodontids, pointed out their resemblance to the mioclaenids, and suggested that the two families might eventually prove to be synonymous. He remarked that they lack diagnostic insectivore specializations and expressed belief that they are closer to the Condylarthra than to the more typical Insectivora. Nevertheless, he then placed

<sup>91</sup> He inadvertently cites Osborn and Earle (1895) as Osborn (1892) and gives the impression that the transfer of the periptychids to the Amblypoda was then proposed.



them in the Insectivora because of their primitive character and because of certain marked differences from the phenacodonts.

In 1915 Matthew reviewed the lower Eocene hyopsodonts, which, for the first time, gave him a good knowledge of their foot structure. He then considered them to be condylarths, confirming his tentative suggestion of 1909. He carefully redefined the Condylarthra and included these five families, the last provisionally: Mioclaenidae, Hyopsodontidae, Phenacodontidae, Meniscotheriidae, and ?Pleurospirotheriidae.

In his last contribution (Pale. Mem.) Matthew retained this arrangement, except that the Mioclaenidae and Hyopsodontidae are reduced by further study to two subfamilies of Hyopsodontidae, as already tentatively foreseen in 1909.

I now propose to return to Cope's arrangement of 1884, with the only change the inclusion of the Hyopsodontidae (with Mioclaeninae), that is, to his classical conception of a group based on both the phenacodonts and the periptychids. It seems to me, after careful and long consideration with practically all the pertinent original specimens (including a good deal even unknown to Matthew), that comprehension of this group has been retarded and taxonomy has been in a blind alley since the rise in the nineties of the idea of close periptychid-pantolambdid affinities, an idea to which even Matthew finally subscribed after some years of resistance. This reactionary view, which at this late date will rather seem radical, requires an outline defense even though much of the crucial evidence is not drawn from the present fauna.

The original suggestion that *Periptychus* might be an amblypod (Osborn and Earle, 1895, p. 47) was based on the facts that its tarsus is not serial and that "it has the strictly trigonal molar of the Amblypoda." It may at once be noted that these arguments have since proved to be valueless. It is now known that the primitive condylarth tarsus was not serial, and the molars of Periptychidae are not, as a rule, strictly trigonal, those of some condylarths are, and the periptychid molars are otherwise decidedly more condylarth- than amblypod-like.

Cope (1897, p. 335) stated that he had anticipated that the periptychids, with their astragalo-cuboid contact (nonserial tarsus), might be the bunodont ancestors of the Amblypoda, but he awaited discovery of their carpus and evidence that it, also, was nonserial. The carpus had not been discovered, but the continuing failure to discover any other possible amblypod ancestry led Cope then to assume the presence of a nonserial carpus in the periptychids and to consider them as this ancestry. He was also influenced by the suggestion of Osborn and Earle. This is too theoretical to warrant much con-

sideration. The periptychid carpus is, in fact, "alternating", but so is that primitive for and apparently fairly common among (other) condylarths.

Osborn (1898, pp. 177-179, 184-186) gives a long list of taligrade characters as defining that group and common to pantolambdids and periptychids. The great majority of these are, as he states, primitive characters. As far as confirmed among the so-called Taligrada by later research, they are also found to occur among or to be equally typical of Condylarthra and hence have no bearing on the particular question here considered. The only progressive taligrade character given is "molars triangular (tritubercular), selenodont", which is decidedly untrue of the Periptychidae and opposed to Osborn's thesis. Indeed, I cannot see that Osborn then advanced any actually valid evidence in favor of the conclusion given, which has since become taxonomic and phylogenetic dogma, largely on his authority.

Matthew (1897) had already shown that even in the supposedly typical condylarths, the phenacodonts, the early forms have alternating, not serial, carpus and tarsus and that the Condylarthra therefore could not be defined and were not characterized by the mooted primitive serial carpus and tarsus as had previously been supposed. He therefore found no difficulty in retaining the Periptychidae in the Condylarthra and gave a lucid and valid argument for doing so, even though, as I now think, he minimized his evidence by much overstressing the resemblance of the periptychids to the pantolambdids in limb structure and their difference from the phenacodonts and mioclaenids in dental pattern.

Upon transferring the Hyopsodontidae to the Condylarthra, Matthew (1915b, p. 311) gave a long diagnosis of the Condylarthra, involving the whole bodily structure. His intention at the time was to exclude the Periptychidae, since he did so in earlier and later general classifications, although this point was not then specifically mentioned, since it was foreign to the fauna he was revising. It is therefore remarkable and significant that his definition of the Condylarthra clearly excludes the Pantolambdidae but applies exactly to, and hence includes, the Periptychidae with a single exception: "tarsals serial." This one point was, in fact, an error or *lapsus*, for the forms he explicitly meant to include do not have strictly serial tarsals, and in some the approach to the periptychids in this respect is very close.

Matthew's subsequent defense of the collocation of Periptychidae and Pantolambdidae was based almost entirely on the limbs, especially on the astragalus. When evidence drawn from the dentition was at variance with that drawn from the limbs or astragalus, he almost invariably followed the latter. Without quarreling with this principle of research, it will appear below that the evidence is not necessarily at variance in the present instance. The dental evidence certainly

favors condylarth rather than amblypod affinities for the periptychids, and the limbs might perhaps support either view equally well and certainly do not oppose condylarth affinities. The recognition of the affinities of *Coriphagus*, as discussed under that genus, adds to the evidence for the opinion supported here.

It has been generally recognized that the teeth of the periptychids could not give rise to those of pantolambdids or coryphodonts. They are in fact aberrant and developing along a line, or series of lines, of their own. It has sometimes been recognized, and can readily be shown, that their greatest resemblance is with the Condylarthra and that they could all be immediately derived from types well known in that order. Indeed, they intergrade with certain mioclaenids to such a point that the families are difficult to distinguish on this basis. The pantolambdid-coryphodont dentitions, on the other hand, are widely different. Union of periptychids and pantolambdids has, then, rested entirely on limb, and especially on foot structure. Indeed, without slighting the fact that other resemblances occur, it has depended more on the astragalus than on any other point. If this arrangement is a natural one, it seems necessarily to imply that the "taligrade" astragalus and limb structure arose in a stock with extremely primitive teeth and that the widely divergent periptychid and pantolambdid dentitions developed later. Such a thesis seems *a priori* rather improbable, but certainly it is not impossible. The apparently, but I think falsely, analogous case of the divergence of, say, suid and camelid dentitions after the artiodactyl foot structure arose suffices to demonstrate that such a history is conceivable.

The analogy is probably false and the thesis indefensible because in the case of the artiodactyls the teeth, followed back in time, distinctly converge and are rather plainly derivable from a common type possessed by animals that already had all the essential artiodactyl limb characters. This is not true of the periptychids and pantolambdids. Even within the limits of the Periptychidae there are forms with hardly any suggestion of the "taligrade" foot, but with teeth much too distinctly periptychid to give rise to the pantolambdids. A common ancestor, if it existed at all, can hardly have had taligrade feet but must almost certainly have been a condylarth and a very primitive condylarth. A review (table 50) of typical astragali of the groups conceived will make the situation clearer.

These genera are all of about the same age. The Hyopsodontidae are represented by isolated Gidley Quarry specimens surely of this group but not exactly determinable, as there are several hyopsodontids of about this size in the quarry. All five genera have numerous other characters of the astragalus in which they are closely similar. These are nondifferentiated primitive protoungulate characters, most of them disappearing in more advanced forms.



TABLE 50.—Review of typical astragali in four genera of Paleocene Condylarthra and a Paleocene pantodont

| Genus                             | Proportions of body and trochlea                   | Astragalar foramen                                                        | Crests                                                                  | Trochlea                                                                 | Internal malleolar facet                                     |
|-----------------------------------|----------------------------------------------------|---------------------------------------------------------------------------|-------------------------------------------------------------------------|--------------------------------------------------------------------------|--------------------------------------------------------------|
| <i>Tetractaenodon</i> .....       | Body broad, trochlea short.                        | In pronounced medial emargination at proximal end of trochlea.            | External crest sharp, internal distinct but rounded.                    | Shallow                                                                  | Not extending so far distally as the trochlea.               |
| Hyposodontid, genus undetermined. | About equidimensional.                             | In pronounced emargination, more on external side.                        | About as in <i>Tetractaenodon</i> , less elevated.                      | Very shallow                                                             | About as in <i>Tetractaenodon</i> .                          |
| <i>Hemithlaeus</i> .....          | Very broad and short.                              | About as in <i>Tetractaenodon</i> .                                       | About as in <i>Tetractaenodon</i> .                                     | About as in <i>Tetractaenodon</i> .                                      | Do.                                                          |
| <i>Periptychus</i> .....          | About equidimensional.                             | Foramen and emargination about as in Hyopsodontidae.                      | About as in Hyopsodontidae.                                             | About as in <i>Tetractaenodon</i> or slightly shallower.                 | Do.                                                          |
| <i>Pantolambda</i> .....          | Equidimensional or slightly broader.               | About as in <i>Tetractaenodon</i> (foramen larger).                       | About as in Mioclaeninae or <i>Periptychus</i> but still less elevated. | Markedly shallower, almost flat.                                         | Extending distal to trochlea, down onto neck.                |
| Genus                             | Plantar processes                                  | Sustentacular facet                                                       | Neck                                                                    | Head                                                                     | Cuboid facet                                                 |
| <i>Tetractaenodon</i> .....       | Small internal and large, sharp external.          | Oval, gently convex, isolated.                                            | Long, oblique, constricted.                                             | Compressed dorsoplantad, articular surface elongate transversely convex. | Very small.                                                  |
| Hyposodontid, genus undetermined. | Similar, but less produced.                        | About as in <i>Tetractaenodon</i> .                                       | About as in <i>Tetractaenodon</i> .                                     | About as in <i>Tetractaenodon</i> .                                      | Apparently slightly larger.                                  |
| <i>Hemithlaeus</i> .....          | About as in <i>Tetractaenodon</i> .                | do                                                                        | Slightly shorter, less constricted.                                     | do                                                                       | About as in Hyopsodontidae.                                  |
| <i>Periptychus</i> .....          | About as in Hyopsodontidae.                        | About as in <i>Tetractaenodon</i> , slightly more flattened and expanded. | About as in <i>Hemithlaeus</i> .                                        | Closely similar to <i>Tetractaenodon</i> , but less compressed.          | Small but distinct, probably larger than in preceding forms. |
| <i>Pantolambda</i> .....          | About as in Hyopsodontidae or <i>Periptychus</i> . | Considerably enlarged, confluent with cuboid facet.                       | Very short, practically absent, not constricted.                        | Slightly depressed, less distal and less convex.                         | Large.                                                       |

All five groups are basically similar in the astragalus. The early Hyposodontidae probably are most primitive in this part, and surely the characters that they share with *Tetraclaenodon* must be taken as primitive. From this point of view, *Pantolambda* is much the most divergent. *Tetraclaenodon* and the early hyposodontids resemble each other very closely, almost the only differences being the greater elevation of the crests and excavation of the trochlea and probably the reduction of the cuboid contact in *Tetraclaenodon*. Both these characters may be incipient specializations, and both are much emphasized in later phenacodonts and not in later members of other groups. The longer, or relatively narrower, body in the hyposodontids is probably of slight significance. *Hemithlaeus* is very close both to *Tetraclaenodon* and the hyposodontids. Its slightly shorter neck, almost its only peculiarity with respect to the more primitive condylarths, can hardly be supposed to make this a "taligrade" astragalus, especially as the shortness is only relative and the neck is, in fact, well developed and typically constricted. The same statement applies to *Periptychus*, the neck of the astragalus being about the same in that genus and definitely more condylarthran than "taligrade" in character. All the other characters of the astragalus are condylarthran except that the cuboid facet is about intermediate between the most primitive known condylarth and amblypod conditions.

*Pantolambda* has a much more primitive astragalus than *Coryphodon*, yet the table clearly shows that it diverges farther from the primitive condylarthran condition than does *Periptychus*. This divergence consists chiefly of the appearance in rudimentary form of characters greatly emphasized in *Coryphodon*. Despite the fact that he himself abandoned it, Matthew's argument of 1897 in favor of considering *Periptychus* as a condylarth and *Pantolambda* as an "amblypod" seems to be as valid now as when he wrote it, indeed more so, for he was not then fully aware of the distinctions between these two genera now brought out.

*Periptychus* does, of course, make some approach toward the so-called amblypods in limb structure, but this is far from reaching identity, and, being only vaguely or not at all seen in smaller contemporaneous allies of *Periptychus*, may indeed be only convergent and largely conditioned by size and mode of locomotion. Convergence is the more likely in such forms that have not in any case come far from a purely primitive type of ungulate limb structure. Similarly *Pantolambda* is much more primitive than *Coryphodon* or other, later allies in limb structure, but it shows the beginning of the so-called amblypod type, and the approach is as much toward all or any primitive ungulates as specifically toward *Periptychus* and its allies. Patterson (1934) has also pointed out that the limb structure of *Barylambda* tends to link *Pantolambda* with the coryphodonts.

The later history of the astragalus and feet in general in these groups is not entirely pertinent but may be mentioned. In the phenacodonts, culminating in *Phenacodus* itself, the limbs became considerably specialized in an inadapative cursorial direction. Side toes were moderately reduced, the limbs became or remained moderately slender, and the feet digitigrade, carpus and tarsus serial. The astragalus differs markedly even from that of the closely allied but earlier *Tetraclaenodon*. The trochlea becomes very long, the foramen and emargination are lost, the crests both become high and sharp, and the head becomes more spherical and loses contact with the cuboid.<sup>92</sup> The hyopsodonts were remarkably conservative. As far as we know them, the limbs of *Hyopsodus* differed extremely little from those of its long antecedent Middle Paleocene relatives. An astragalus of *Hyopsodus* from the Eocene is almost identical with that of a Paleocene hyopsodontid here described except for the quite unimportant details of having the body somewhat less elongate and the head slightly more spherical. The Anisonchinae and Periptychinae have no known descendents after this stage (except for a few scraps in the early Upper Paleocene apparently not generically different from those of the Middle Paleocene). The amblypod astragalus became very markedly modified in *Coryphodon*. Its limbs are highly graviportal throughout, and the astragalus is profoundly modified and convergent toward some other graviportal types.

The present conception of this order is as follows:<sup>93</sup>

#### Order CONDYLARTHRA:

##### Family Hyopsodontidae:

|                          |                                            |
|--------------------------|--------------------------------------------|
| Subfamily Mioclaeninae   | } Members of a persistently very primitive |
| Subfamily Hyopsodontinae |                                            |

group. Small, possibly insectivorous (in habits, not affinities) animals with simple, low-crowned, bunodont teeth and clawlike unguals. This longest-lived group is also in almost all respects the least specialized. Lower Paleocene to upper Eocene. North America.

Family Phenacodontidae: A progressively more cursorial and probably more strictly herbivorous group, generally analogous within this much more primitive and nonadaptive radiation to the early progressive ungulates (especially perissodactyls) that replace them in the Eocene. Teeth brachyodont, becoming polybunus with some slight tendency toward lophiodonty. Lateral toes becoming somewhat reduced and unguals flattened into hoofs. Middle Paleocene to lower Eocene. North America, South America, Europe.

<sup>92</sup> Some of these characters were supposed to be typical of the Condylarthra, because *Phenacodus* was the only adequately known genus when the order (or suborder, then) was first defined, and it may seem strange to consider *Phenacodus* as a peculiar and in many respects atypical condylarth. It is, in some sense of the word, technically a "type" of the Condylarthra, but it is definitely not typical throughout. Taxonomy has many such cases in which a natural group was recognized and named, even though in the first instance it was largely based on a form later found to be marginal in it.

<sup>93</sup> Matthew has given excellent diagnoses of all the groups concerned. These characterizations are meant to be explanatory, not formally diagnostic.



## Order CONDYLARTHRA—Continued.

Family Periptychidae: Characterized by persistently plantigrade feet and by teeth markedly bunodont, the premolars not becoming molariform (as in other families) but evolving independently into large swollen crushing teeth, the molars relatively small, with the primary cusps conical and crowded together, developing a peculiar type of polybuny especially in the upper teeth by the development of new cuspules largely internal to the primary cusps.

Subfamily Anisonchinae: Small and slender forms with the basic dental characters of this family, but the teeth relatively simple and general structure apparently closely similar to the Hyopsodontidae. Lower to Middle Paleocene. North America.

Subfamily Periptychinae: Larger subgraviportal forms developing heavy limbs and somewhat amblypodlike feet, with complex, polybunous molars. Lower to Upper Paleocene. North America.

Family Meniscotheriidae: Hyracoidlike animals of middle size with lopho- or buno-selenodont teeth, serial carpus and tarsus, and narrow, hooflike unguals. Their early history is unknown and their relationships doubtful. They may not be very close to the other condylarths. Their dental evolution seems to have been in a direction distinct from any other primitive ungulates, and almost opposite that of the periptychids, but could have started from a common basis in the Paleocene.

Subfamily Meniscotheriinae: Typical, more lophiodont forms. Uppermost Paleocene and lower Eocene. North America.

Subfamily Pleuraspidothériinae: More bunodont forms, of still more dubious position. Upper Paleocene. Europe.

In the present fauna the Hyopsodontidae are very abundant and varied. Phenacodonts are present but are not abundant, being especially rare in the quarry facies. Anisonchines are not uncommon but are limited in variety, only two genera and species being recognized, and are much less common or varied than in the Puerco and Torrejon. The Periptychinae, so common in the San Juan Basin faunas, appear to be wholly lacking. Meniscotheres are absent, as would be expected since this group is known only from younger strata.

## Family HYOPSODONTIDAE Lydekker, 1889

The small Paleocene animals now believed to be condylarths allied to *Hyopsodus* have had a confusing and complex history, which is here to be sketched only in its more essential points. Cope's genus *Mioclaenus* was at first referred by him to the Condylarthra, but he later removed it to the Creodonta on the basis of the skeletal characters of "*Mioclaenus*" *ferox*. He referred many species to the genus, making it a sort of dumping ground for unspecialized dentitions of more or less bunodont, tubercular-sectorial type. Schlosser, in 1886, suggested that *Mioclaenus* might really be a condylarth (as Cope originally supposed). Scott (1892) separated out a number of Cope's species and placed them in distinct genera. "*M.*" *ferox* was then made the basis for the genus *Claenodon*, a true creodont. Scott then considered that true *Mioclaenus*, really allied to the type *M. turgidus*,

might be a condylarth genus, in which case "it will form a very distinct family of that order."

Osborn and Earle (1895) placed *Mioclaenus* in the Condylarthra and proposed a new family Mioclaenidae. They discussed only *M. turgidus* and evidently intended to include in the family only *Mioclaenus* and in that genus only the few species not definitely removed by Scott. Matthew (1897) hesitated in regarding the Mioclaenidae as condylarthrs but did leave them in that group. He placed in the genus *Mioclaenus* the species *Tricentes inaequidens* Cope, which Scott (1892) had made type of the genus *Ellipsodon*, and he proposed a new genus *Protoselene* for *Mioclaenus opisthacus* Cope.

In their 1895 paper, Osborn and Earle described a new genus *Oxyacodon*, listed as *incertae sedis* but in the vicinity of the creodonts. Matthew (1897) left the genus as *incertae sedis* and transferred to it *Anisonchus agapetillus* Cope. In 1914, in a faunal list, Matthew transferred *Oxyacodon* to the Mioclaenidae, with a footnote that it might be a periptychid. In his subsequent work (see Pale. Mem.) Matthew confirmed the association of *Oxyacodon* with *Mioclaenus* and transferred to it the other Puerco species, "*Mioclaenus*" *turgidunculus*, thus confining the genus *Mioclaenus* (*sensu stricto*) to the Middle Paleocene. He also revived *Ellipsodon* Scott and placed in it *Mioclaenus acolytus* Cope and *Mioclaenus lemuroides* Matthew.

The arrangement reached by Matthew is thus as follows:

|          |                      |                                                                                   |
|----------|----------------------|-----------------------------------------------------------------------------------|
| Puerco:  | <i>Oxyacodon</i>     | Type: <i>O. apiculatus</i> .                                                      |
|          |                      | Referred: <i>O. agapetillus</i> , <i>O. turgidunculus</i> , <i>O. priscilla</i> . |
| Torrejon | <i>Mioclaenus</i>    | Type: <i>M. turgidus</i> .                                                        |
|          |                      | Referred: <i>M. lydekkerianus</i> .                                               |
|          | <i>Ellipsodon</i>    | Type: <i>E. inaequidens</i> .                                                     |
|          |                      | Referred: <i>E. lemuroides</i> , <i>E. acolytus</i> .                             |
|          | <i>Protoselene</i> : | Type: <i>P. opisthacus</i> .                                                      |

The history of the Eocene group Hyopsodontidae has been sufficiently noticed in connection with the discussion of the Condylarthra as whole. Matthew early recognized that the hyopsodontids and mioclaenids were related and in 1909 suggested that future discovery might result in merging the two supposed families. In his Paleocene memoir he took this step, retaining the earlier double grouping in the form of two subfamilies, Hyopsodontinae with *Haplomylus* and *Hyopsodus* and Mioclaeninae with the earlier genera listed above.

After Matthew's work numerous discoveries of new hyopsodontids have been made. Jepsen (1930) described *Litolestes* and *Fhena-codaptus* from the Upper Paleocene of Wyoming. He placed the former doubtfully in the Insectivora and the latter doubtfully in the Artiodactyla, but I have already suggested (Simpson, 1936b) that they are probably hyopsodontids. Finally there are three new

genera of hyopsodontids in the present fauna, *Haplaletes*, *Litomylus*, and *Litolestes*. The number of known genera has nearly doubled since Matthew completed his work, and the whole unwieldy group requires reconsideration. The genera now known and considered hyopsodontid are as follows:

*Choeroclaenus* (defined below): Type *C. turgidunculus*. Lower Paleocene.  
*Oxyacodon*: Type *O. apiculatus*. Lower Paleocene.  
*Mioclaenus*: Type *M. turgidus*. Middle Paleocene.  
*Ellipsodon*: Type *E. inaequidens*. Middle Paleocene.  
*Protoselene*: Type *P. opisthacus*. Middle Paleocene.  
*Litales*: Type *L. disjunctus*. Middle Paleocene.  
*Litomylus*: Type *L. dissentaneus*. Middle Paleocene.  
*Haplaletes*: Type *H. disceptatrix*. Middle Paleocene.  
*Litolestes*: Type *L. ignotus*. Upper Paleocene.  
*Phenacodaptes*: Type *P. sabulosus*. Upper Paleocene.  
*Haplomylus*: Type *H. speirianus*. Uppermost Paleocene and Lower Eocene.  
*Hyopsodus*: Type *H. paulus*. Lower to Upper Eocene.

The types and many other specimens of these genera have been examined for the present work <sup>94</sup> in order fully to analyze the affinities of the Fort Union forms here described and their contribution to knowledge of the family.

In the first instance, generic designations were disregarded and the 18 well-defined Paleocene species referable to this family were graphically compared by a tabulation of all their known characters.<sup>95</sup> They were found to fall naturally into groups that correspond very well with the various genera recognized by Matthew and those defined after his work. The principal characters distinguishing these generic groups are shown in the following key, which also gives (in parentheses) the species now placed in each genus, the type being indicated by an asterisk.

#### KEY TO THE PRINCIPAL GENERA OF HYOPSODONTIDAE KNOWN IN THE PALEOCENE

- I. Paraconids internal, fusing with metaconids; entoconids indistinct, fusing with hypoconulids.
  - A. P<sub>4</sub> enlarged, inflated, few accessory cuspules.
    1. Paraconids less internal, entoconid distinct on M<sub>2</sub>, few or no crenulations, M<sub>3</sub> large, with projecting hypoconulid, M<sup>3</sup> with large metacone-----**Choeroclaenus** <sup>96</sup> (*turgidunculus*\*)
    2. Paraconids wholly internal, entoconid indistinguishable on M<sub>2</sub>, crests crenulated. M<sub>3</sub> much reduced, with rounded heel. Metacone vestigial on M<sup>3</sup>-----**Mioclaenus** (*turgidus*\*)

<sup>94</sup> Material of *Litolestes* and *Phenacodaptes* through the courtesy of Dr. G. L. Jepsen. The American Museum collections include most of the types and many excellent specimens of all the genera except *Phenacodaptes*. The type specimen of *Hyopsodus paulus* was not seen, but many good specimens of this and other species of *Hyopsodus* were examined.

<sup>95</sup> Two or three poorly known supposed species of doubtful status were omitted.

<sup>96</sup> New genus, defined on p. 232.



B.  $P_4$  cuspidate, more or less enlarged but not inflated.

3.  $P_4$  without distinct paraconid, metaconid absent or rudimentary, talonid relatively wider,  $M_3$  much to somewhat reduced.

**Ellipsodon** (*inaequidens*\*, *priscus*, *lemuroides*, *acolytus*, *aquilonius*)

4.  $P_4$  with rudimentary paraconid, metaconid relatively large, talonid narrow,  $M_3$  relatively large.....**Litaletes** (*disjunctus*\*)

II. Paraconids median to subinternal, not fusing with metaconids, entoconids distinct, molar talonids basined.

- C. Teeth more lophiodont,  $P_4$  bicrescentic, paraconids distinct,  $P^1$  with metacone,  $M^{1-2}$  with strong mesostyle,  $M_3$  large.

5.....**Protoselene** (*opisthacus*\*)

- D. Teeth more bunodont, paraconids reduced or vestigial, no mesostyles,  $M_3$  generally somewhat reduced.

- a.  $P_4$  without distinct paraconid, but relatively elongate and trenchant,  $M_3$  large, with projecting hypoconulid, molar cusps acute.

6.  $P_4$  with rudimentary metaconid, molar paraconids relatively large.....**Oxyacodon** (*apiculatus*\*, *agapetillus*, *priscilla*)

7.  $P_4$  with distinct metaconid, with a pit between this and protoconid, molar paraconids reduced...**Litomylus** (*dissentaneus*\*)

- b.  $P_4$  with distinct small paraconid but relatively wide and heavy,  $M_3$  somewhat reduced, molars bunodont, generally broad and low.

8.  $P_4$  with smaller metaconid and talonid, talonid of  $M_3$  less elongate, upper molars more transverse and angulate, outer cusps of  $P^{3-4}$  more compressed.

**Litolestes** (*ignotus*\*, *notissimus*)

9. Metaconid and talonid of  $P_4$  larger,  $M_3$  more elongate,  $P^{3-4}$  with more conical outer cusps, upper molars rounded and less transverse.....

**Haplaletes** (*disceptatrix*\*)

- c.  $P_4$  elongate, with strong paraconid,  $M_3$  reduced, prominent cingulum descending from protocone tip.

10.....**Haplomylus** (*speirianus*\*)

Like all keys, this is artificial, but it is based on an extensive analysis of the characters of all the species listed, and an effort has been made to select characters that have clear taxonomic value and are probable or possible indications of phyletic relationships. Thus it is believed to be probable that the capital letters indicate four natural groups of genera. The primary division, indicated by Roman numerals, also appears to me (but with somewhat less probability) to be a natural dichotomy of the whole group.

Matthew has suggested that *Choeroclaenus turgidunculus*, which he referred to *Oxyacodon*, might be ancestral to one or more species of *Ellipsodon*. The resemblance is certainly close, and I believe a relationship to exist. It seems to me, however, to be that indicated above by group I and hence more general than he suggested and inclusive of *Mioclaenus*, *sensu stricto*. In more exact phyletic relationship, *Choeroclaenus turgidunculus* appears to be closer to *Mioclaenus turgidus*. The resemblance in the molars is as close as to *Ellipsodon*,

and the premolars are practically those of *Mioclaenus* in miniature and unlike those of *Ellipsodon*. Furthermore, the rather poorly known *Ellipsodon priscus* carries that genus, or something very like it and probably closely related, back into the Lower Paleocene, contemporaneous with *Choeroclaenus*.

The group of species referred to *Ellipsodon* is rather heterogeneous, as discussed under that genus. The presence of so many varied species shows that several divergent minor phyla are present, but all appear to be rather closely allied. *Ellipsodon priscus* represents a possible ancestral type of structure, without being clearly allied to any particular one of the Middle Paleocene species. The other species are all approximately contemporaneous and so represent a spreading out of the group without permitting the discernment of any special lines of descent.

*Oxyacodon* represents the second major group in the Lower Paleocene. Its distinctive characters are almost entirely primitive and it affords a structural ancestry for its general group, *D*. It is improbable that the ancestry of *Protoselene* would enter into *Oxyacodon*, and the case of *Haplomylus* is also dubious. Upper teeth of *Oxyacodon* are unknown, and might considerably modify the present conception of the genus.

*Litomylus* very closely resembles *Oxyacodon* but is in at least two respects, molarization of  $P_4$  and reduction of molar paraconids, a more advanced form. As far as the scanty data go, it could be a relatively unprogressive descendant of *Oxyacodon*.

*Haplaletes* and *Litolestes*, both possible structural derivatives of *Oxyacodon*, are successive, Middle and Upper Paleocene, respectively, and appear to be close relatives, but they cannot be along exactly the same line of descent, at least in the known species. *Litolestes*, the later genus, is probably more specialized in the reduction of  $M^3_3$  and perhaps in the more transverse upper molars, compression of  $P^{3-4}$ , and some other details, but its premolars seem to be slightly but distinctly less progressive than in *Haplaletes*. (Its known species are also somewhat smaller than *Haplaletes disceptatrix*.)

*Haplomylus* appears at the end of the Paleocene and runs into the lower Eocene. It is clearly a member of this general group, but none of the older genera is enough like it to suggest any very close structural ancestry. Its general premolar and molar structure, although somewhat more advanced as would be expected, is of the type of group *D* of the foregoing key and is such impelling evidence of relationship that the genus has been classed with that group. At the same time some important details are not foreshadowed in any of the other genera. The most striking point, the development of the posterointernal part of the upper molars as a broad cingulum sweeping down from the protocone, curiously reminiscent of some of the ancient primates, is approached (but not very closely) in

*Ellipsodon*, but the other characters of the dentition almost exclude the possibility of special relationship.

*Protoselene* is a more sharply defined genus than any of the others here considered. It has the general characters of a primitive hyopsodontid but is evidently becoming specialized throughout the dentition in a way hardly suggested by any other genus.

*Hyopsodus* is not inserted in the above key, because it is not known in the Paleocene and because it is so distinctive that it can be recognized at a glance, and confusion with the Paleocene genera is impossible. This distinctive character, however, is entirely in features demonstrably progressive, and anyone who studies the whole structure of *Hyopsodus*, particularly with reference to the evolution that occurred within that genus, can hardly fail to endorse Matthew's conclusion that it is an ally of the Paleocene forms here discussed. The genera discovered since Matthew's work still more strongly substantiate the reality of this relationship, for it may now be said that *Hyopsodus* has no known structural character not clearly developed or adumbrated in the Paleocene hyopsodontids.<sup>97</sup>

*Hyopsodus* most nearly resembles group *D* of the foregoing key, and in a general way this group has every essential requirement for the structural ancestry of the Eocene genus. Its most exact resemblance in details appears to be with *Haplaletes*. The sequence *Oxyacodon-Haplaletes-Hyopsodus* is, as far as it is known, one in which no difficulty opposes its acceptance as a structural phylum. There are no "crossing specializations", and all characters seem to be modified uniformly and in one direction in accord with the relative ages of the genera. At the same time it is, of course, apparent that the data are inadequate to prove that this is an exact genetic phylum, and, as in most cases, the probabilities are very much against our having in collections the exact members of the true line of descent.

There remains for discussion only *Phenacodaptes* Jepsen, 1930. This has not been inserted in the key because its affinities with the other genera are not definitely established, and Dr. Jepsen has material that he has not yet described and that may give a better basis for decision. From his published data, the genus appears to me to enter into the Hyopsodontidae. It has characters strongly suggestive of the dichobunid artiodactyls, but so has the whole Paleocene group of hyopsodontids. It is, indeed, almost impossible to frame a diagnosis, on dental characters alone, that will surely distinguish hyopsodontids and artiodactyls, yet such skeletal parts as are known show that they were quite distinct, at least in the lower Eocene, and even the dentitions give a definite feeling, supported

<sup>97</sup> Mlle. Friant's recent reference of *Hyopsodus* to the Insectivora and strange discussion of the derivation of insectivore, especially erinaceoid, molar patterns can be quite ignored. She seems to be wholly unaware of any of the evidence for the true affinities of *Hyopsodus*.



by distinctions open to exception but fairly distinctive with the whole group in mind, that they are different groups. Whether it be considered as a dichobunid or as a hyopsodontid, *Phenacodaptes* is a peculiar form. Yet all its characters known to me are either duplicated or rather closely approached by various hyopsodontids, and its reference to that group is at least as probable as any other view. The fact that no artiodactyl, or no other artiodactyl, is known from the Paleocene in itself carries no great weight as regards the affinities of *Phenacodaptes*, except from the point of view of logical procedure in the special case. If, as seems to me to be true, *Phenacodaptes* resembles a group that is known to have been abundant and varied when it lived at least as closely as it resembles another that has never been found in deposits of that age, it seems preferable to refer it to the former group pending discovery of decisive evidence.

If *Phenacodaptes* should prove to be a hyopsodontid, it will not very closely enter any of the categories of the key, not so much that it has any nonhyopsodontid character as that it is a synthetic type. The lower premolars are somewhat more suggestive of group *I*, although they could well appear also in group *II*. The molar trigonids, as far as I can judge by the data known to me, may be either *Ellipsodon*- or *Haplaletes*-like, probably the former, but the entoconids are more as in *Haplaletes* and its allies.

Suprageneric grouping of these forms has always been based on a separation of *Hyopsodus* from all other known forms. Historically it is easy to see how this arose and that it was logical to the point of being the only arrangement permitted by the data. *Hyopsodus* is, within this group, an advanced genus with pronounced modifications, tending to conceal its relationships to the very primitive forms. Even within the genus, knowledge was principally based on relatively late (especially middle Eocene) and specialized species. Furthermore the only Paleocene forms adequately known were from the Lower and Middle Paleocene and were typified by such a form as *Mioclaenus turgidus*, which lies rather far from the structural ancestry of *Hyopsodus*.

Even Matthew necessarily based his conception of the genus on forms that suggest marked separation from *Hyopsodus* within the family. Aside from *Mioclaenus* he knew only *Oryacodon*, *Ellipsodon*, *Protoselene* (with *Haplomylus* in latest Paleocene and early Eocene). *Oryacodon* is so ancient and primitive that intermediate stages were necessary to show its probable phyletic position. *Ellipsodon* now appears to lie nearer *Mioclaenus*, at least in its typical species, than to the more *Hyopsodus*-like genera. *Protoselene* is curiously divergent and not very near any other genus. He regarded *Haplomylus* as to some extent intermediate between the earlier forms and *Hyopsodus*, and probably this largely influenced him in uniting the Hyopsodon-

tidae and Mioclaenidae, but he saw that *Haplomylus* could not be ancestral to *Hyopsodus* and was not clearly derivative from any known Paleocene form, so that the evidence was inconclusive.

The discovery, since Matthew, of several Middle and Upper Paleocene genera that are clearly related to *Mioclaenus* and *Ellipsodon* but that approach *Hyopsodus* much more closely than do those two genera has much altered the conception of this family. It is now seen that in the Paleocene there are a less *Hyopsodus*-like and a more *Hyopsodus*-like group. The distinction of the Hyopsodontinae, with *Hyopsodus* only, depended in part on progressive characters, sure to become uncharacteristic when forms of intermediate age and structure were found, and in part on what appear to be valid phyletic characters which separate *Hyopsodus* from one group of Paleocene genera, but associate it with the other. On present data, it seems preferable to base supergeneric classification on these latter characters and to draw the line not between the Paleocene forms and *Hyopsodus* but between those of the Paleocene forms that are less and more like *Hyopsodus*, grouping that genus with its closer relatives among the older genera.

Subfamilies drawn upon this basis are defined below. This arrangement is still only tentative, and it is clear from the discussion of generic relationships above that a great deal must yet be learned before a really well-founded classification within the family will be possible, but the new arrangement perhaps represents a step toward this end. The most doubtful points, as regards the forms now known, are the affinities of the more atypical species placed in *Ellipsodon* and of *Litaletes*, the true place in the system of the rather isolated genus *Protoselene*, that of the apparently aberrant *Haplomylus*, and the relationships of *Phenacodaptes*.

The new evidence substantiates without greatly altering the grounds for considering the hyopsodontids as condylarths, sufficiently set forth by Matthew. Discovery of intermediate forms makes the family more coherent than it seemed to him and improves the evidence for considering the relatively well known *Hyopsodus* as indicative of the affinities of the Paleocene genera, and so strengthens his conclusions. The resemblance of the early hyopsodontids to the dichobunids in the dentition is so remarkably close that it is difficult to ascribe it entirely to convergence. Although the known skeletal parts are not of artiodactyl type, it is quite possible that some branch of the earliest hyopsodontids did give rise to the Artiodactyla, but this can be proved or disproved only by further discovery. Even if this should prove to be the case, the hyopsodontids as a whole would probably be best classified as Condylarthra, since they had the general characters of that order, and retained them after the ancestral artiodactyls were distinctly differentiated in the skeleton.

Subfamily MIOCLAENINAE Matthew (ex ms.) (Mioclaenidae Osborn and Earle, 1895)

*Revised definition.*—Paleocene hyposodontid condylarths with  $P_4^1$  more or less enlarged and sometimes inflated.  $P_4$  generally relatively simple, with small talonid. Molar paraconids reduced, internal, fusing with metaconids. Molar talonids generally open, entoconids reduced, fusing with hypoconulid and becoming vestigial.  $M_3^3$  often more or less reduced.  $M^{1-2}$  with very weak or no hypocone, posterior cingulum tending to run to tip of protocone.

This subfamily is redefined to include *Mioclaenus*, its structural ancestor *Choeroclaenus*, *Ellipsodon*, and (doubtfully) *Litaletes*, and to exclude *Protoselene*, *Oxyacodon*, and some other genera formerly placed in it. *Choeroclaenus* does not occur in the fauna here under discussion, but it is defined below because reconsideration of the whole family demands the proposal of this new name. *Ellipsodon* and *Litaletes* have species in this fauna and are further considered in connection with these species.

**CHOEROCLAENUS<sup>98</sup>, new genus**

*Type.*—*Mioclaenus turgidunculus* Cope, 1888.

*Distribution.*—Lower Paleocene, Puerco, New Mexico.

*Diagnosis.*— $P_4^1$  bulbous, inflated.  $P_4$  without anterior cuspule, paraconid or metaconid, talonid very small, with one faintly crested cuspule. Molar paraconids small but distinct, nearly confluent with metaconids but not wholly internal. Entoconids distinct and about as high as hypoconulids, molar talonids basined.  $M_3^3$  little or not reduced.  $M_3$  with projecting hypoconulid.  $M^{1-3}$  transverse, with sharp external, anterior, and posterior cingula. Hypocone indistinct, posterior cingulum tending to connect with protocone tip.  $M^3$  with well-developed metacone. Conules small, distinct. Cusps low but sharp and clear-cut, crenulations and proliferation of minor cuspsules slight or absent.

*Discussion.*—The type species rather closely resembles the type of *Mioclaenus*, *M. turgidus*, and has almost invariably been referred to that genus.<sup>99</sup> It is, however, sharply distinguished by the characters given above and in the key on a previous page. Most of these distinctions are primitive characters, and they tend to link this form, more nearly than the later and more aberrant *Mioclaenus turgidus*, to the small and more generalized early hyposodontids. Matthew, the only person who had critically examined the specimens since Cope, recognized this and recorded it (Pale. Mem.) by transferring the species to the primitive genus *Oxyacodon*, a structurally defensible and reason-

<sup>98</sup> *Xoīpos*, pig, + *claeus*, a combination meant to suggest the dental resemblance to bunodont artiodactyls, relationship to *Mioclaenus*, and derivation from the Puerco beds.

<sup>99</sup> The single exception, previous to Matthew's last work, seems to be Roger, who placed it in *Protagonodon* in his catalog, but the reason for this is not apparent.



able assignment. Our present greatly expanded knowledge of Middle Paleocene hyopsodontids, however, throws emphasis on certain characters that now appear to be more important phyletically than those previously apparent. The premolar inflation is unlike *Oxyacodon* both in kind and degree and points toward *Mioclaenus*, s. s., and not *Ellipsodon*. In the lower molars the position, shape, and connections of the paraconid are very much unlike *Oxyacodon* and point toward *Mioclaenus* and *Ellipsodon* rather than toward *Litomylus* and *Haplalestes* (described since Matthew's death) as does *Oxyacodon*. The entoconids are, indeed, distinct, an *Oxyacodon*-like character, but they are definitely fusing with the hypoconulid and do not suggest continued independence as in the group to which *Oxyacodon* belongs. (No Middle Paleocene genus known to Matthew belonged to this group, although it is now richly represented, and so he could not evaluate the importance of this character.) The upper teeth are not known in true *Oxyacodon*, but the characters of the lower teeth sharply distinguish *Choeroclaenus* from that genus.

#### Genus ELLIPSODON Scott, 1892

This genus is revised in Matthew's memoir. It is unusually varied in structure, and the species here referred to it increases this variety. *Ellipsodon aquilonius*, of this fauna, closely resembles *E. acolytus*. The latter is fairly close to *E. lemuroides*, which in turn approaches *E. inaequidens*. There is no logical or convenient separation, probably of more than specific rank, in this series of four species, yet *E. aquilonius* is markedly unlike *E. inaequidens*, which is the type of the genus. Whether any generic or subgeneric separation is proper, must depend on future discovery. At present it seems that the genus may be too broadly drawn, but this is not demonstrated unequivocally, and it probably is a natural genus in the sense that the species referred to it are related to each other.

The type species, *E. inaequidens*, is poorly known. The type specimen is a palate with  $P^3$ - $M^3$  of one side or both, all the teeth deeply worn, and the palate encased in hard concretion. Another palate is less worn, but even more obscured by concretion, and a third shows  $M^{1-2}$  fairly well preserved. Lower jaw fragments reveal  $P_4$ - $M_3$ . All the few surely referable specimens were collected by Baldwin for Cope in 1882 to 1885, and the great collections made subsequently contain only one specimen possibly referable to the species, and this one is highly dubious. As far as their localities are recorded, Baldwin's specimens all came from Gallegos Canyon, and it is possible that they are from some local pocket worked out by him or not well exposed when later collectors visited the area. The unusual circumstance that the type is the poorest known species of the genus and has not turned up in new collections for over 50 years makes the status of the

genus somewhat uncertain. The structure of  $P_4$ , the extreme reduction of  $M_3$ , and perhaps some less clear details are peculiar with respect to *E. lemuroides* or *E. acolytus*, and the fact that the genus is known principally from these atypical species may mean that its true nature, as based on *E. inaequidens*, is now seriously misunderstood.

In general aspect, *E. aquilonius* resembles some of its associates such as *Litaletes disjunctus* more than it does *Ellipsodon inaequidens*, but in structural detail it seems closer to *Ellipsodon acolytus* and is conservatively associated with that species generically (rather than definitely with the type of *Ellipsodon*).

ELLIPSODON AQUILONIUS Simpson

FIGURES 62, 63

*Ellipsodon aquilonius* SIMPSON, 1935d, p. 242.

*Type*.—U.S.N.M. no. 9280, right lower jaw with  $P_3$ – $M_3$  and alveoli. Collected by A. C. Silberling.

*Paratype*.—U.S.N.M. no. 9567, right upper jaw with  $P^3$ – $M^2$ . Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Types from Gidley Quarry, surely referable specimens from Silberling Quarry and one, more doubtful, from Loc. 51, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Close to *E. acolytus* in size and structure, but teeth generally slightly slenderer,  $P_4$  relatively shorter and with metaconid more distinct.  $M^3_3$  only moderately reduced.  $P^3$  without protocone.  $M^{1-2}$  with rudimentary hypocone not connected to protocone apex. Measurements given below.

*Discussion*.—This is one of the commonest species in the quarries and is represented by a fine series of specimens revealing its dental morphology and variation in detail, although in no case is the anterior dentition preserved.

The number of incisors is unknown. The post-incisive dentition was complete numerically.

The upper canine and  $P^1$  are unknown.  $P^2$  is a small simple tooth with a small anterior and a larger posterior root. The crown is compressed, trenchant, with a median cusp, minute posterior cuspsule, and posterointernal cingulum.  $P^3$  has three roots but is longer than wide and has only one distinct cusp, which is central and is triangular in section, with minute anterior and posterior basal cuspsules and a sharp, continuous, but not cuspidate internal cingulum, stronger on the posterointernal than on the anterointernal face.  $P^4$  is wider than long and has a strong protocone, which is, however, lower than the amphicone. There is no separate metacone. The amphicone is triangular and has a sharp posterior and a weak anterior crest from

the tip. There is a distinct parastyle and small vague metastyle. The entire crown is circled by a cingulum which bears a cusp, topographically a metaconule, near the middle of the posterior border.

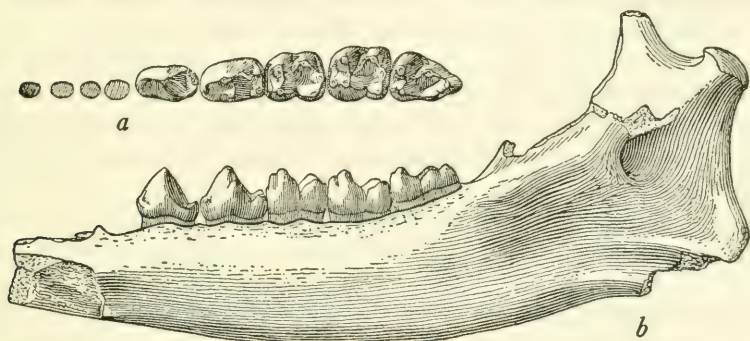


FIGURE 62.—*Ellipsodon aquilonius* Simpson, U.S.N.M. no. 9280, right lower jaw: *a*, Crown view; *b*, internal view. Two and one-half times natural size.

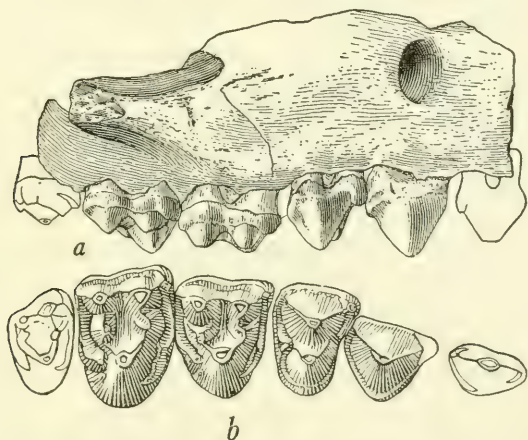


FIGURE 63.—*Ellipsodon aquilonius* Simpson, U.S.N.M. no. 9567, with parts in outline supplied from U.S.N.M. nos. 9571 and 9576; left upper jaw: *a*, External view; *b*, crown view. Four times natural size.

M<sup>1</sup> and M<sup>2</sup> have the same structure but differ in size and proportions. Although distinct, the paracone and metacone are crested and the crests tend to form a simple ectoloph. The protocone is crescentic and its wings bear definite protoconules and metaconules, just internal to paracone and metacone. There is a sharp, continuous external cingulum, small definite parastyle, very vague metastyle, and no mesostyle. The pronounced anterior cingulum stops short at the anterointernal corner without rising or rounding the long internal slope of the protocone. The otherwise similar posterior cingulum



risers toward the protocone apex at the inner end and terminates in a definite point, a rudimentary hypocone on the posterior protocone slope and near, but separate from, the protocone tip.  $M^3$  is oval, with rounded corners, and is reduced but much less so than in *E. inaequidens*. It has a vestigial but distinct metacone.

The lower canine is known only from its single, cylindrical root, which indicates a small tooth (but larger than  $P_1$ ) only slightly procumbent.  $P_1$  has one small root and a slightly procumbent and recurved simple crown, excavated on the posterointernal face.  $P_2$  is considerably larger, 2-rooted, and with a single distinct heel cusp.  $P_3$  is transitional to  $P_4$  in structure, with the heel considerably expanded and a curved crest and excavation at the anterointernal angle.  $P_4$ , although sharply distinct from the molars, is more nearly molariform than in any other species referred to this genus. There is a low distinct metaconid on the posterointernal protoconid slope, at about two-thirds of the distance from the base to the apex of the crown. The anterointernal protoconid slope is excavated, and the anterior protoconid crest curves inward and then posteriorly around it, generally without forming a cusp but in a few specimens with a very rudimentary and low paraconid. The talonid has a slight crest ending in a cusp at the posterior margin, somewhat external to the midline, with a vague, open internal basin and a small posterointernal cuspsule.

$M_1$  has the protoconid and metaconid opposite, the metaconid slightly the larger of the two. The paraconid is distinct, fully internal, partly connate with the metaconid, and smaller and lower than the latter. The talonid is nearly as high as the trigonid and is well basined, but with the basin open in a narrow notch between entoconid and metaconid. The hypoconid is large, distinct and crescentic. The small hypoconulid and larger and equally high entoconid are poorly separated. When quite unworn, three small cuspsules are seen, one on the anterior hypoconid wing, one on the posterior metaconid slope, and one on the anterior entoconid crest. The talonid is wider than the trigonid.  $M_2$  is similar to  $M_1$ , but the trigonid is larger, absolutely and relatively, and is as wide as or wider than the talonid. The entoconid is reduced in size, in height, and in distinction and the talonid basin more open.  $M_3$  is reduced, the trigonid decidedly the widest part of the tooth, the entoconid indistinct, and the hypoconulid large and sharply projecting as a well-defined spur.

U.S.N.M. no. 9686 preserves  $dm_4$ . Its talonid closely resembles that of  $M_1$  but is smaller. The trigonid is much more elongate and narrow than on the permanent molars, and the paraconid is larger and well separated from the metaconid.

The horizontal ramus is slender, with a long symphysis, which seems not to have fused even in old age. The posterior mental

foramen is generally beneath the posterior end of  $P_3$  or anterior end of  $P_4$ . The coronoid process seems to have been high and broad. The masseteric fossa is shallow and simple, its only sharp boundary anterior. The angle is poorly preserved but evidently was rounded and not sharply projecting. The dental foramen is about on a level with the alveolar border. The condyle is elevated well above the teeth and its transversely oval, gently convex articular surface faces equally posteriorly and superiorly.

The infraorbital foramen is above  $P^3$ , and the zygoma arises chiefly above  $M^2$ .

The statistical constants of the principal tooth dimensions are given in table 51, based entirely on the sample from the Gidley Quarry.

TABLE 51.—Numerical data on upper and lower dentition of *Ellipsodon aquilonius*

| Variate      | N  | R       | M                | $\sigma$          | V             |
|--------------|----|---------|------------------|-------------------|---------------|
| $LP_3$ ----- | 10 | 2.8-3.5 | $3.22 \pm 0.06$  | $0.19 \pm 0.04$   | $6.0 \pm 1.3$ |
| $WP_3$ ----- | 10 | 1.7-2.1 | $1.88 \pm 0.03$  | $0.108 \pm 0.024$ | $3.7 \pm 0.8$ |
| $LP_4$ ----- | 10 | 3.2-3.7 | $3.41 \pm 0.05$  | $0.16 \pm 0.04$   | $4.6 \pm 1.0$ |
| $WP_4$ ----- | 11 | 2.1-2.5 | $2.31 \pm 0.04$  | $0.116 \pm 0.025$ | $5.0 \pm 1.1$ |
| $LM_1$ ----- | 19 | 3.1-3.6 | $3.40 \pm 0.03$  | $0.143 \pm 0.023$ | $4.2 \pm 0.7$ |
| $WM_1$ ----- | 19 | 2.7-3.2 | $2.90 \pm 0.04$  | $0.172 \pm 0.028$ | $5.9 \pm 1.0$ |
| $LM_2$ ----- | 28 | 3.1-3.9 | $3.58 \pm 0.03$  | $0.179 \pm 0.024$ | $5.0 \pm 0.7$ |
| $WM_2$ ----- | 29 | 2.8-3.6 | $3.30 \pm 0.04$  | $0.190 \pm 0.025$ | $5.8 \pm 0.8$ |
| $LM_3$ ----- | 24 | 3.5-4.1 | $3.82 \pm 0.03$  | $0.134 \pm 0.019$ | $3.5 \pm 0.5$ |
| $WM_3$ ----- | 24 | 2.4-3.0 | $2.75 \pm 0.03$  | $0.161 \pm 0.023$ | $5.8 \pm 0.8$ |
| $LP^3$ ----- | 6  | 3.1-3.3 | $3.23 \pm 0.03$  | $0.075 \pm 0.022$ | $2.3 \pm 0.7$ |
| $WP^3$ ----- | 7  | 2.5-2.9 | $2.71 \pm 0.06$  | $0.15 \pm 0.04$   | $5.4 \pm 1.4$ |
| $LP^4$ ----- | 7  | 3.0-3.2 | $3.11 \pm 0.024$ | $0.064 \pm 0.017$ | $2.1 \pm 0.6$ |
| $WP^4$ ----- | 7  | 3.8-4.1 | $3.96 \pm 0.04$  | $0.12 \pm 0.03$   | $3.0 \pm 0.8$ |
| $LM^1$ ----- | 10 | 3.1-3.4 | $3.21 \pm 0.03$  | $0.104 \pm 0.023$ | $3.3 \pm 0.7$ |
| $WM^1$ ----- | 10 | 4.1-4.5 | $4.29 \pm 0.05$  | $0.14 \pm 0.03$   | $3.4 \pm 0.8$ |
| $LM^2$ ----- | 13 | 3.1-3.7 | $3.43 \pm 0.05$  | $0.17 \pm 0.03$   | $4.9 \pm 1.1$ |
| $WM^2$ ----- | 13 | 4.9-5.4 | $5.20 \pm 0.05$  | $0.17 \pm 0.03$   | $3.2 \pm 0.6$ |
| $LM^3$ ----- | 8  | 2.3-2.6 | $2.40 \pm 0.04$  | $0.100 \pm 0.025$ | $4.2 \pm 1.0$ |
| $WM^3$ ----- | 9  | 3.5-4.1 | $3.71 \pm 0.07$  | $0.21 \pm 0.05$   | $5.6 \pm 1.3$ |

Despite the fact that the sample probably includes both sexes and certainly includes teeth in many different stages of wear, the figures are very consistent and show remarkably little variation. The highest V is only 6.0 and the average is 4.35. The consistent distribution of the V's is also striking, for of the 20 values only two differ from the average by as much as twice the corresponding standard error. The two exceptions (for length of  $P^3$  and length of  $P^4$ ) are based on scanty data and are abnormally low values, 2.3 and 2.1.

The unusually adequate sample of *E. aquilonius* from the Gidley Quarry and the presence of seven lower jaws apparently of the same species from the Silberling Quarry afford the best opportunity to detect any minor differences that might occur between these two horizons and localities. The possible association of morphological

variants with one locality or the other and possible differences in mean dimensions have been carefully compared. The greatest difference in mean dimensions is only 0.2 mm (for width of  $P_3$ ), which is not shown to be significant (it being mathematically demonstrable that a difference as great would arise in random sampling of a homogeneous sample about once in 20 trials or oftener). The other differences are far from any probable significance. Only one specimen from the Silberling Quarry falls outside the observed range for the Gidley Quarry in a single dimension, having  $M_1$  3.8 mm in length, but this is far within the probable range of the Gidley Quarry population, the deviation being only 1.4 times the standard deviation.

It is unnecessary to give the results of the numerous other detailed comparisons made, since all were negative, showing no significant difference between the samples from the two quarries. Since the samples are so good, this warrants the positive affirmation that a single race of this species occurs in both quarries.

A single specimen from Loc. 51, U.S.N.M. no. 9709, a lower jaw with  $M_1$  and broken  $M_2$ , has these two teeth above the average size for the Gidley Quarry sample, but within the range of the latter.

#### ELLIPSODON species

U.S.N.M. no. 9662, from Loc. 18, is a partial right lower jaw with  $P_4$ . This tooth resembles that of *Ellipsodon aquilonius* but is relatively higher, the paraconid is more distinct, and the length, 4.2 mm, is significantly greater than in that species ( $d/\sigma=4.9$ ), although the width, 2.6 mm, is not ( $d/\sigma=2.5$ ). This is probably another species, but the material is inadequate for its exact determination.

#### Genus LITALETES Simpson

*Litaletes* SIMPSON, 1935d, p. 242.

*Type*.—*Litaletes disjunctus* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.— $P_4$  with bladelike main cusp, distinct paraconid and relatively large metaconid, talonid small with narrow, rudimentary, open basin. Molar paraconids distinct, small, internal. Entoconids indistinct, fusing with hypoconulids, especially on  $M_2$ .  $P^4$  with rudimentary metacone, strong metastyle.  $M^{1-2}$  with distinct hypocones.  $M^3$  not reduced,  $M^3$  with strong metacone.

*Discussion*.—This genus is very distinct from *Ellipsodon*, but *Litaletes disjunctus* and *Ellipsodon aquilonius* do not differ very greatly. It could hardly be supposed that *Ellipsodon inaequidens*, type of that genus, is congeneric with *Litaletes disjunctus*, for their whole adaptive tendency seems different, and each tooth has definite and pronounced structural distinctions. The question then is not whether *Ellipsodon* and *Litaletes* are distinct genera, but where the



more or less transitional *Ellipsodon aquilonius* belongs. It is closer to *Ellipsodon acolytus* than to *Litaletes disjunctus* or any other species known to me, and, as already stated, that is the reason for referring it to *Ellipsodon* at present. It is, however, probably closer to *Litaletes disjunctus* than to *Ellipsodon inaequidens*. Perhaps it will be necessary to transfer *E. aquilonius* and *E. acolytus* to *Litaletes* at some future time, but that introduces a great difficulty as regards the generic position of *E. lemuroides*, and for the present the system adopted here seems equally natural and more convenient.

## LITALETES DISJUNCTUS Simpson

FIGURES 64, 65

*Litaletes disjunctus* SIMPSON, 1935d, p. 242.

*Type*.—U.S.N.M. no. 9323, right lower jaw with C-M<sub>3</sub> (M<sub>3</sub> broken). Collected by A. C. Silberling.

*Paratype*.—U.S.N.M. no. 9324, right upper jaw with P<sup>3</sup>-M<sup>3</sup>. Collected by A. C. Silberling.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Sole known species of genus. Measurements given in table 52.

*Discussion*.—P<sup>3-4</sup> and M<sup>1</sup> of the species are now known only from the paratype, so that their variation is not established. On this specimen both P<sup>3</sup> and P<sup>4</sup> have distinct parastyle and metastyle and on both the posterior amphicone crest bears a rudimentary metacone, larger on P<sup>4</sup>. P<sup>3</sup> has a rudimentary protocone. On P<sup>4</sup> the metaconule is not developed on the cingulum but more normally, on the protocone wing, and the cingulum does not cross the inner face of the protocone. On M<sup>1-2</sup> the parastyle is unusually prominent and the hypocone is larger than in *Ellipsodon aquilonius* and not so near the protocone apex. M<sup>3</sup> is less reduced, less oval, and the metacone, although smaller than the paracone, is large and distinct.

TABLE 52.—Available numerical data on lower teeth of *Litaletes disjunctus* from the Gidley Quarry

| Variate               | N | R         | M     | Σ(d) <sup>2</sup> |
|-----------------------|---|-----------|-------|-------------------|
| LP <sub>3</sub> ----- | 3 | 3. 3-3. 5 | 3. 37 | 0. 0267           |
| WP <sub>3</sub> ----- | 3 | 1. 9-2. 1 | 2. 00 | 0. 0200           |
| LP <sub>4</sub> ----- | 5 | 3. 5-3. 9 | 3. 68 | 0. 1080           |
| WP <sub>4</sub> ----- | 5 | 2. 4-2. 8 | 2. 54 | 0. 1120           |
| LM <sub>1</sub> ----- | 7 | 3. 9-4. 2 | 4. 07 | 0. 0743           |
| WM <sub>1</sub> ----- | 5 | 3. 2-3. 5 | 3. 30 | 0. 0800           |
| LM <sub>2</sub> ----- | 6 | 4. 3-5. 2 | 4. 67 | 0. 5134           |
| WM <sub>2</sub> ----- | 5 | 3. 7-4. 5 | 4. 04 | 0. 3520           |
| LM <sub>3</sub> ----- | 3 | 5. 0-5. 3 | 5. 13 | 0. 0467           |
| WM <sub>3</sub> ----- | 4 | 3. 3-3. 8 | 3. 55 | 0. 1700           |

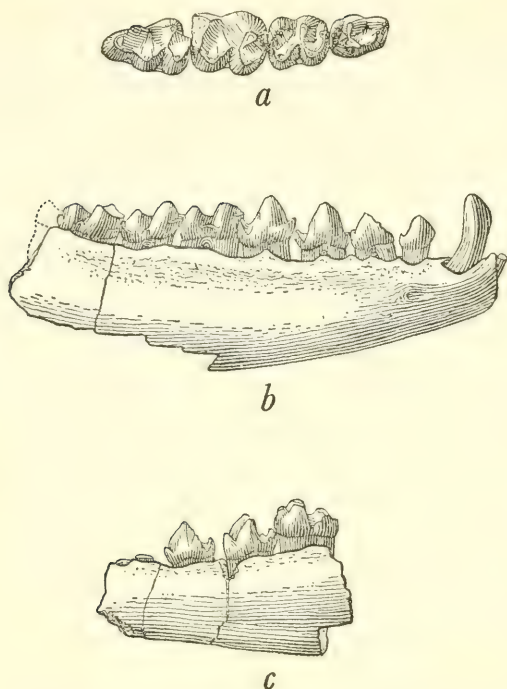


FIGURE 64.—*Litaletes disjunctus* Simpson: a, U.S.N.M. no. 9281, right  $P_4$ - $M_3$ , crown view; b, U.S.N.M. no. 9323, right lower jaw, external view; c, U.S.N.M. no. 9338, right lower jaw, internal view. Twice natural size.

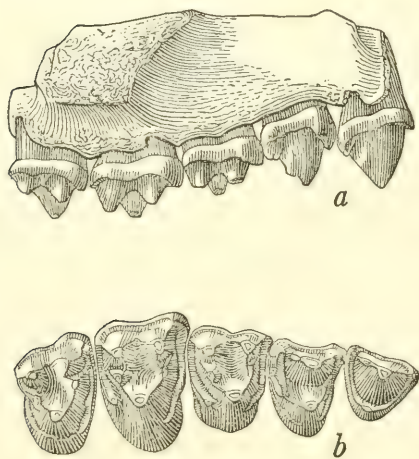


FIGURE 65.—*Litaletes disjunctus* Simpson, U.S.N.M. no. 9324, right upper jaw: a, External view; b, crown view. Three times natural size.

The lower canine is a small but tall, erect, spatulate tooth.  $P_1$  is low, 1-rooted, with a minute heel.  $P_{2-3}$  are more advanced than in *Ellipsodon* in that each has a distinct paraconid. The heel is, however, relatively short, and only half its width is formed by the incipient basin. The anterior blade of the protocone is distinctively modified into a sort of shearing crest.

The lower molars closely resemble those of *Ellipsodon aquilonius*, but  $M_1$  has trigonid and talonid of nearly equal width,  $M_2$  has trigonid generally markedly wider, and  $M_3$  is less reduced.

U.S.N.M. no. 6179 from Loc. 51, includes an  $M_2$  morphologically comparable to this species and measuring 4.7 by 3.9 mm, near the means for the Gidley Quarry specimens. There is, however, an upper jaw with  $M^{2-3}$  from the same locality, dimensions given in table 53, that is morphologically very close to this species but notably smaller than the available Gidley Quarry specimens. Since, however, these are only two in number it cannot be assumed that a real difference exists. The greatest relative difference, in length of  $M_2$ ,

does not necessarily imply a coefficient of variation higher than 5 on the hypothesis that a single species is present, and this is a very moderate degree of variation for one species.

TABLE 53.—Measurements (in mm) of available upper teeth of *Litaletes disjunctus*

| U.S.N.M. no.              | P <sup>3</sup> |     | P <sup>4</sup> |     | M <sup>1</sup> |     | M <sup>2</sup> |     | M <sup>3</sup> |     |
|---------------------------|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
|                           | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   |
| 9324 (Gidley Quarry)----- | 3.4            | 2.8 | 3.3            | 4.4 | 3.9            | 5.0 | 4.6            | 6.2 | 3.6            | 5.3 |
| 9582 (Gidley Quarry)----- |                |     |                |     |                |     | 4.8            | 6.5 | 3.4            | 5.6 |
| 9660 (Loc. 51)-----       |                |     |                |     |                |     | 4.0            | 5.6 | 3.1            | 5.1 |

### Subfamily HYOPSODONTINAE Trouessart, 1879<sup>1</sup>

*Revised definition.*—Paleocene and Eocene hyopsodontid condylarths with P<sup>4</sup> not inflated, generally moderate in size, cuspidate, somewhat molariform but never exactly so, P<sub>4</sub> generally with a metaconid and wide but imperfect talonid basin. Molar paraconids median to subinternal, not fusing with metaconids, entoconids distinct and high, talonid basins closed. M<sup>3</sup><sub>3</sub> little or not reduced. M<sup>1-2</sup> with definite hypocone, small in earlier and large in later forms, sharply distinct from tip of protocone.

*Remarks.*—Aside from the type genus, I place here *Oxyacodon*, *Litomytus*, *Litolestes*, and *Haplaletes* with some assurance, *Protoselene* and *Haplomytus* very doubtfully. *Litomytus* and *Haplaletes* represent the subfamily in the present collection.

#### Genus LITOMYLUS Simpson

*Litomytus* SIMPSON, 1935d, p. 243.

*Type.*—*Litomytus dissentaneus* Simpson.

*Distribution.*—Middle Paleocene, Fort Union, Montana.

*Diagnosis.*—P<sub>4</sub> trenchant, paraconid rudimentary, metaconid distinct, separated from the protoconid by a small pit. Molar cusps rather bunodont but acute, paraconids reduced and median, M<sup>3</sup><sub>3</sub> little reduced, hypoconulid of M<sub>3</sub> sharply projecting. Hypocones of M<sup>1-2</sup> relatively large and internal. M<sup>3</sup> transverse, triangular.

#### LITOMYLUS DISSENTANEUS Simpson

FIGURE 66, 67

*Litomytus dissentaneus* SIMPSON, 1935d, p. 243.

*Type.*—U.S.N.M. no. 9425, left lower jaw with P<sub>3</sub>–M<sub>3</sub>. Collected by A. C. Silberling.

<sup>1</sup> "Hyopsodontinae" in the original publication, but the emendation can hardly be claimed to change authorship.



*Horizon and locality.*—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis.*—Sole known species of genus. Dimensions given in table 54.

*Discussion.*—This is the rarest of the four species of hyopsodontids in the quarry, but it is distinctive and fairly well known.

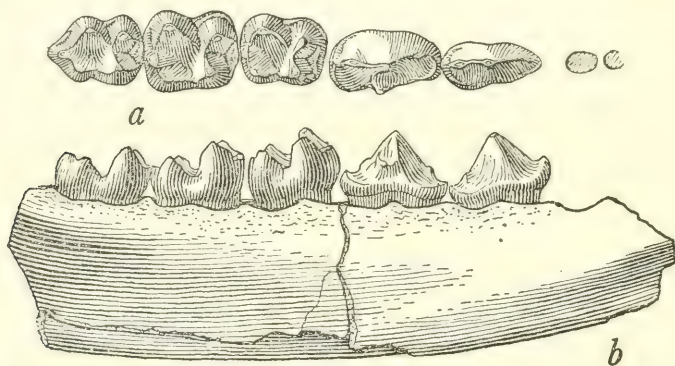


FIGURE 66.—*Litomytus dissentaneus* Simpson, U.S.N.M. no. 9425, left lower jaw: a, Crown view; b, internal view. Four times natural size.

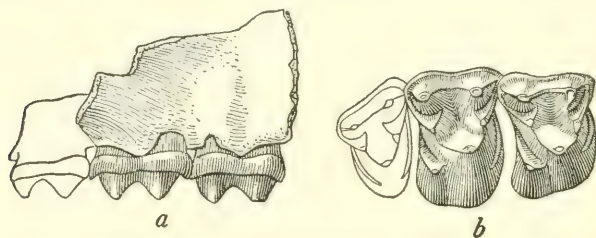


FIGURE 67.—*Litomytus dissentaneus* Simpson, U.S.N.M. no. 9557, with tooth in outline from U.S.N.M. no. 9580, right  $M1-3$ : a, External view; b, crown view. Four times natural size.

No upper teeth anterior to  $P^4$  are known, and  $P^4$  is represented only by an uncharacteristic fragment.  $M1-2$  have sharp, subequal, nearly conical paracone and metacone. The protocone is likewise sharp and smaller than in the other species of this group. The conules are large and equal. The external cingulum is sharp and even forming equal angulations, rather than distinct cusps, at the parastylar and metastylar corners. There is no mesostyle. The hypocone is larger than in any known contemporaneous species and is quite distinct from the protocone and equally internal, but smaller.  $M^3$  is markedly transverse and is triangular, not rounded or oval, without a hypocone but with a sharp, distinct metacone.

$P_{3-4}$  are long, low, narrow, trenchant teeth, unlike any others known in this family. Each has a rudimentary, median, basal paraconid. The talonids are poorly developed in each case and have only a single posteromedian cuspsule and a very rudimentary posterointernal basin.

The sharp posterior protoconid crest bears a very slight thickening or cuspule. The anterointernal region is somewhat excavated and has a cingulum below it.  $P_3$  has no metaconid, but  $P_4$  has a small papilla about halfway up the crown, and above and external to it, between it and the protoconid apex, is a small pit or pocket.

The lower molars, with their acute, well-separated major cusps, resemble those of *Oxyacodon*. The paraconids are vestigial, forming a small shelf or crest connected with the anterior protoconid wing but not with the metaconid. On  $M_1$  this nearly reaches the inner border, on  $M_2$  it is submedian, and on  $M_3$  fully median. Protoconid and metaconid are of nearly equal size. The heels are well basined and the entoconids are sharp and distinct, nearly as high as the hypoconids and on  $M_{1-2}$  larger and higher than the small hypoconulids. On  $M_3$  the hypoconulid is as high as the hypoconid and projects sharply posteriorly.

Only five specimens, all from the Gidley Quarry, are recognized as of this species. Measurements are given in table 54.

TABLE 54.—Individual measurements (in mm) of upper and lower dentition of *Litomytus dissentaneus*

| U.S.N.M.<br>no. | $P_3$ |     | $P_4$ |     | $M_1$ |     | $M_2$ |     | $M_3$ |     |
|-----------------|-------|-----|-------|-----|-------|-----|-------|-----|-------|-----|
|                 | L     | W   | L     | W   | L     | W   | L     | W   | L     | W   |
| 9425.....       | 3.3   | 1.7 | 3.5   | 1.9 | 2.9   | 2.4 | 3.0   | 2.7 | 3.2   | 2.2 |
| 9318.....       |       |     |       |     | 2.9   | 2.1 | 3.0   | 2.5 | 3.4   | 2.2 |
| 9536.....       | 3.6   | 1.6 | 3.9   | 1.7 |       |     |       |     |       |     |

| U.S.N.M. no. | $M^1$ |     | $M^2$ |     | $M^3$ |     |
|--------------|-------|-----|-------|-----|-------|-----|
|              | L     | W   | L     | W   | L     | W   |
| 9557.....    | 3.2   | 4.2 | 3.3   | 4.7 |       |     |
| 9580.....    | 2.9   | 3.9 | 3.2   | 4.5 | 2.6   | 4.1 |

### Genus HAPLALETES Simpson

*Haplaletes* SIMPSON, 1935d, p. 243.

*Type*.—*Haplaletes disceptatrix* Simpson.

*Distribution*.—Middle Paleocene, Fort Union, Montana.

*Diagnosis*.— $P_4$  not trenchant, with distinct paraconid and metaconid and relatively large basined heel. Molars bunodont, cusps rather rounded and low. Paraconids reduced and median.  $M_3^3$  somewhat reduced, hypoconulid of  $M_3$  slightly projecting, markedly less than in *Litomytus*. Amphicones of  $P^{3-4}$  more rounded than in *Litolestes*.  $P^4$  with rudimentary metacone. Upper molars rounded. Hypocones of  $M^{1-2}$  distinct, but smaller than in *Litomytus*.  $M^3$  less transverse and more rounded.

## HAPLALETES DISCEPTATRIX Simpson

FIGURES 68, 69

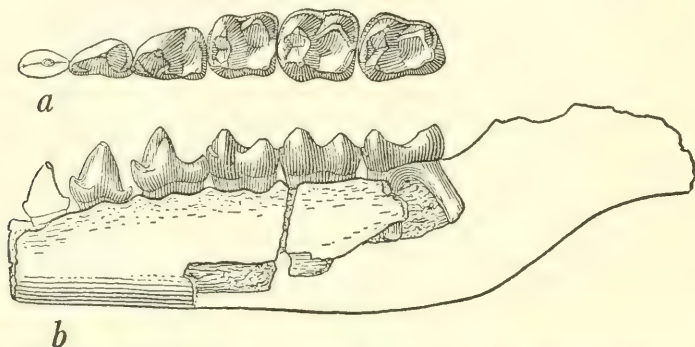
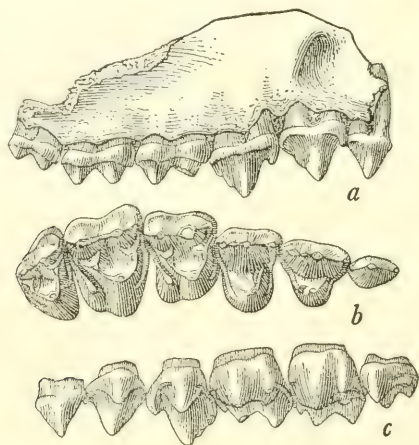
*Haplaletes disceptatrix* SIMPSON, 1935d, p. 244.*Type*.—U.S.N.M. no 9500, right lower jaw with  $P_3$ – $M_3$ . Collected by A. C. Silberling.*Paratype*.—U.S.N.M. no. 9555, right upper jaw with  $P^2$ – $M^3$ . Collected by Dr. J. W. Gidley.FIGURE 68.—*Haplaletes disceptatrix* Simpson, U.S.N.M. no. 9500, with parts in outline supplied from U.S.N.M. no. 9600, right lower jaw: a, Crown view; b, internal view. Four times natural size.FIGURE 69.—*Haplaletes disceptatrix* Simpson, U.S.N.M. no. 9555, right upper jaw: a, External view; b, crown view; c, internal view. Four times natural size.*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.*Diagnosis*.—Sole known species of genus. Dimensions in tables 55 and 56.*Discussion*.—This delicate little species is the smallest condylarth in the quarries, and only *Litolestes* includes smaller known species in this order.



TABLE 55.—Principal available numerical data on lower dentition of *Haplaletes disceptrix*, all from the Gidley Quarry

| Variate               | N | R         | M     | $\Sigma(d^2)$ |
|-----------------------|---|-----------|-------|---------------|
| LP <sub>3</sub> ----- | 3 | 2. 1-2. 3 | 2. 20 | 0. 0200       |
| WP <sub>3</sub> ----- | 3 | 1. 3-1. 5 | 1. 40 | 0. 0200       |
| LP <sub>4</sub> ----- | 2 | 2. 5      | 2. 5  | 0             |
| WP <sub>4</sub> ----- | 2 | 1. 6-1. 7 | 1. 65 | 0. 0050       |
| LM <sub>1</sub> ----- | 4 | 2. 4-2. 6 | 2. 48 | 0. 0276       |
| WM <sub>1</sub> ----- | 4 | 2. 1-2. 3 | 2. 18 | 0. 0276       |
| LM <sub>2</sub> ----- | 6 | 2. 4-2. 9 | 2. 65 | 0. 1350       |
| WM <sub>2</sub> ----- | 6 | 2. 3-2. 7 | 2. 51 | 0. 1066       |
| LM <sub>3</sub> ----- | 6 | 2. 6-2. 9 | 2. 80 | 0. 0800       |
| WM <sub>3</sub> ----- | 6 | 2. 2-2. 4 | 2. 31 | 0. 0286       |

TABLE 56.—Measurements (in mm) of the two available upper dentitions of *Haplaletes disceptrix*, both from the Gidley Quarry

| U.S.N.M. no. | P <sup>2</sup> |     | P <sup>3</sup> |     | P <sup>4</sup> |     | M <sup>1</sup> |     | M <sup>2</sup> |     | M <sup>3</sup> |     |
|--------------|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|----------------|-----|
|              | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   | L              | W   |
| 9555-----    | 1.5            | 1.1 | 2.2            | 2.1 | 2.4            | 2.9 | 2.4            | 3.2 | 2.6            | 3.7 | 1.9            | 3.1 |
| 9556-----    |                |     |                |     | 2.2            |     | 2.5            | 3.1 | 2.9            | 3.7 |                |     |

P<sup>2</sup> is a small simple tooth resembling an anterior lower premolar. P<sup>3</sup> is peculiar in having a low and small but sharp and distinct protocone. P<sup>3-4</sup> resemble those of *Litaletes* in their rudimentary metacones, but the metastyles are less developed, and P<sup>4</sup> has no metaconule. The upper molars are similar to those of *Litomylus*, but are more rounded in contour and have the hypocones of M<sup>1-2</sup> smaller.

P<sub>3</sub> has a distinct paraconid and a heel about as well developed as that of P<sub>4</sub> in most contemporaneous species. P<sub>4</sub> has definite paraconid and metaconid and a wide, large, basined heel with two posterior cusps. The lower molars resemble those of *Litomylus*, but the crowns are lower, the cusps blunter, and the internal cusps more distinctly elevated over the external. The talonid of M<sub>3</sub> is less elongate.

#### Family PHENACODONTIDAE Cope, 1881

Most of the manuscript notes left by Dr. Gidley refer to this group, and it was evidently his intention to publish a preliminary paper on it. There are three different drafts of part of his brief account, evidently written at different times and in part not consistent with one another. The draft that seems to be most recent is still incomplete and has still later memoranda written on it for other changes that were never made. The integral publication of this manuscript is impossible, as it does not form a connected whole and does not fairly

represent the final opinions of Dr. Gidley. I have, however, quoted parts of the manuscript directly, have mentioned some other of Dr. Gidley's opinions in indirect quotation, and have used his manuscript names and followed his disposition of the specimens as far as possible.

The material has been much increased since Dr. Gidley's study of it, but it is still rare. He tentatively identified only 8 specimens, and 11 have since been collected (3 for the National Museum and 8 for the American Museum). This family is abundant in the Torrejon, and also in the lower Eocene, but it is extremely rare in the quarries in the Crazy Mountain Field and can be considered as common only at one surface locality, no. 25, from which 11 specimens have been obtained.

In the Torrejon the only genus of this family is *Tetraclaenodon*.<sup>2</sup> It is there very abundant and highly varied and has therefore received numerous specific names, but from Matthew's work it seems probable that only two valid species occur in the Torrejon: *Tetraclaenodon puercensis*, a larger, more common, and varied form, and *T. pliciferus*, a smaller, rarer, and perhaps less varied species.

In the Crazy Mountain Field, also, there are indications of two species, one of about the size of *T. puercensis*, but very rare and not exactly identifiable, the other smaller, although generally larger than *T. pliciferus*. There is also a second genus, *Gidleyina*, apparently characteristic of the higher levels in this field.

#### TETRACLAENODON Scott, 1892

##### TETRACLAENODON SYMBOLICUS Gidley

FIGURES 70, 71

*Tetraclaenodon symbolicus* GIDLEY, Simpson, 1935d, p. 239.

*Type*.—U.S.N.M. no. 6169, part of right lower jaw with  $M_1$  and alveoli of  $P_{3-4}$  and  $M_2$ . Collected by A. C. Silberling.<sup>3</sup>

*Paratype*.—U.S.N.M. no. 6168, jaw fragment with right  $M_{1-2}$ , and a separate left  $P_4$  probably this species but probably not associated. Collected by A. C. Silberling.

<sup>2</sup> This genus is still often called *Euprotogonia*. It was originally described as *Protogonia* Cope, 1881. Cope later considered this as preoccupied by *Protogonius* Hübner, 1816, and replaced it by *Euprotogonia* Cope, 1893, the type of both being *P. (or E.) subquadrata*. In the meantime Scott had proposed the genus *Tetraclaenodon* Scott, 1892, for *Mioclaenus flowerianus* Cope. Scott did not recognize the relationship, but his *Tetraclaenodon* was certainly the same genus as *Protogonia* Cope, and it therefore includes as a synonym *Euprotogonia* Cope. Matthew in 1897 preferred *Euprotogonia* Cope, 1893, to *Tetraclaenodon* Scott, 1892, on the ground that the latter was based on an error, and through Matthew's work *Euprotogonia* became the familiar name for the genus. Matthew later recognized that his action had been invalid, and he used the name *Tetraclaenodon* in all his more recent work. Now Cabrera (1935) has insisted that *Protogonius* Hübner does not preoccupy *Protogonia* Cope, since they differ in termination, and he calls the genus *Protogonia*. Without taking a decisive stand, I shall tentatively continue to use *Tetraclaenodon*, which has the cardinal virtue of being generally and correctly understood and of being unambiguous. *Euprotogonia* is certainly invalid, and *Protogonia* is of dubious validity, is ambiguous, and is unfamiliar to present-day students.

<sup>3</sup> I retain this specimen as type, since it is clearly that intended by Gidley. No. 6168, here made paratype, would be a better type.

*Horizon and locality.*—Type from Silberling Quarry, paratype from Loc. 25, about 250 feet lower stratigraphically, Fort Union, Middle Paleocene horizon, Montana.

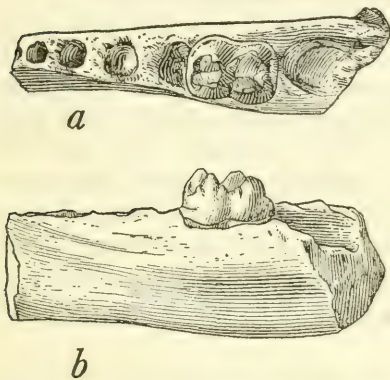


FIGURE 70.—*Tetracaelonodon symbolicus* Gidley, U.S.N.M. no. 6169, right lower jaw (with  $M_1$ ): a, Crown view; b, internal view. One and one-half times natural size.

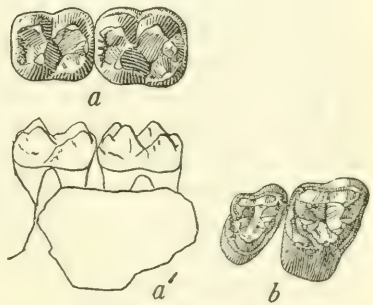


FIGURE 71.—*Tetracaelonodon symbolicus* Gidley; a, U.S.N.M. no. 6168, right  $M_{1-2}$ , crown view; a', same internal view; b, Princeton Univ. no. 13757, right  $M_{1-2}$ , crown view. One and one-half times natural size.

*Diagnosis.*—Gidley: "This species is smaller than *E. [Tetracaelonodon, G. G. S.] puercensis*, being about intermediate in size between that species and *E. minor* [= *Tetracaelonodon pliciferus*, G. G. S.]. The lower molars are proportionately narrower transversely than those of the former species,<sup>4</sup> and the lower jaw is much shallower. This last character may be due in part, however, to a less mature condition of the specimen, which represents a young individual with the first true molar just coming into use.<sup>5</sup> The striking similarity in detail of the lower molars with those of *E. [T., G. G. S.] puercensis* is a notable feature of the species and separates it clearly from *E. minor* [*T. pliciferus*, G. G. S.]. The more notable points of similarity are the slight roughening and wrinkling of the enamel surface and a tendency of the lophs of the teeth to break up into small cuspules."<sup>6</sup>

Simpson: Intermediate between *T. pliciferus* and *T. puercensis* in size, but nearer the former both in size and in structure. The only constant difference from *T. pliciferus* is the greater size, inadequate for specific differentiation were it not constantly correlated with the

<sup>4</sup> And within the range of *T. pliciferus* in this proportion.—G. G. S.

<sup>5</sup> A specimen of *T. pliciferus* of comparable age has a deeper jaw, despite its smaller teeth but a referred specimen of *T. symbolicus* also has a deep jaw. This is probably a highly variable character, and also depends on crushing to a considerable degree.—G. G. S.

<sup>6</sup> From figures of the Torrejon specimens this would seem a striking and good distinction, but the specimens themselves show that *T. pliciferus* also has wrinkled enamel and a tendency for lophs to break up into cuspules. These may be functions of size, to a limited extent, and slightly less pronounced in *T. pliciferus* than in *T. puercensis*. *T. symbolicus* is about intermediate between the two in these characters, as in size.



widely different geographic distribution, as far as known. Crenulations possibly slightly more developed and paraconid weaker on type and paratype of *T. symbolicus*, but these are variable characters and other specimens suggest that they are not of specific value.

*Discussion.*—This species seems to be variable, and it is difficult to separate it from *T. pliciferus*, with which it must be closely related. Its smallest variants, indeed, could not be separated from *T. pliciferus* were they found together, but the homogeneous sample from Loc. 25 averages larger than *T. pliciferus*. Since all these individuals are from one horizon and locality they evidently represent either one herd or an actually interbreeding stock, the character of which is thus slightly different from the Torrejon species and may be given taxonomic distinction. The size difference is statistically significant. I therefore accept Dr. Gidley's species, but consider it as much closer to *T. pliciferus* than he believed.

It happens that the type and to less degree the paratype have the enamel unusually crenulated and the paraconids small, characters slightly closer to *T. puercensis* than to *T. pliciferus*, although those species intergrade in this respect. The other specimens from Loc. 25, however, have the enamel somewhat smoother and the paraconids more distinct, almost exactly as in *T. pliciferus*.<sup>7</sup>

The more recently discovered specimens include one with  $dm_4$ , representatives of all the lower molars and of  $P_2$  and  $P_4$ , and also  $M^{2-3}$ . These are all morphologically within the range of *T. pliciferus*. They might be grouped into three subdivisions, large, medium, and small, but I think the grouping would be subjective and that the variation is individual and approximately normal.

TABLE 57.—Numerical data on lower molars of *Tetraclaenodon symbolicus*

| Variate               | N | R         | M           | $\sigma$    | V         |
|-----------------------|---|-----------|-------------|-------------|-----------|
| LM <sub>1</sub> ----- | 6 | 7. 4-7. 9 | 7. 63±0. 07 | 0. 18±0. 05 | 2. 4±0. 7 |
| WM <sub>1</sub> ----- | 6 | 5. 6-6. 6 | 6. 23±0. 13 | 0. 31±0. 09 | 5. 0±1. 4 |
| LM <sub>2</sub> ----- | 6 | 7. 5-8. 2 | 7. 77±0. 10 | 0. 24±0. 07 | 3. 0±0. 9 |
| WM <sub>2</sub> ----- | 6 | 6. 2-7. 0 | 6. 75±0. 12 | 0. 30±0. 09 | 4. 5±1. 3 |
| LM <sub>3</sub> ----- | 6 | 7. 3-8. 1 | 7. 70±0. 10 | 0. 25±0. 07 | 3. 3±0. 9 |
| WM <sub>3</sub> ----- | 6 | 5. 2-5. 7 | 5. 37±0. 08 | 0. 20±0. 06 | 3. 8±1. 1 |

The available material (including that in the American Museum) provides only six well-preserved examples of each of the three lower molars, and it is not entirely homogeneous since the type and one other specimen (as given below) are not from Loc. 25, whence all other

<sup>7</sup> One of the most extreme specimens in this respect, U.S.N.M. no. 6167, was referred to *T. symbolicus* by Gidley, in his notes, so that his conception of the species was the same as mine despite the differences in the diagnosis.

specimens were derived. Nevertheless the material is well unified, and data on it can be more adequately summed up in statistical form than otherwise. (Table 57.)

The dimensions of the two specimens not from Loc. 25 are given in table 58.

TABLE 58.—*Individual measurements (in mm) of lower molars of Tetraclaenodon symbolicus*

| U.S.N.M. no. | M <sub>1</sub> |     | M <sub>2</sub> |       | M <sub>3</sub> |     |
|--------------|----------------|-----|----------------|-------|----------------|-----|
|              | L              | W   | L              | W     | L              | W   |
| 6169-----    | 7.9            | 6.3 |                |       |                |     |
| 9925-----    | 7.5            | 6.6 | -----          | ----- | 7.9            | 5.7 |

These are to some extent marginal, as might be expected. The type, from the Silberling Quarry, has the largest M<sub>1</sub> recorded, but a specimen from Loc. 25 approaches this within 0.1 mm. No. 9925, from Loc. 3, has the widest M<sub>1</sub> and M<sub>3</sub> recorded, but these two dimensions are approached within 0.2 and 0.1 mm, respectively, by Loc. 25 specimens. The variation is low for the whole series in any event, and there is no reason to believe it heterogeneous as to race.

The close approach of this species to *T. pliciferus* is shown by the dimensions of M<sub>1</sub> of the type of the latter, length 7.5, width 6, within the range of *T. symbolicus* but slightly below the mean. The most readily measurable of the types of *T. "minor"* = *T. pliciferus*, Amer. Mus. no. 3897, has the following dimensions: Length M<sub>1</sub>, 6.8; width M<sub>1</sub>, 5.6; length M<sub>2</sub>, 7.0; width M<sub>2</sub>, 6.2.

This is somewhat more representative of the smaller Torrejon species than is the type of *T. pliciferus*, which is a large variant. The lengths are below and the widths at the observed lower limits for *T. symbolicus*, and the differences are significant.

Princeton no. 13757, from Loc. 9, one of the rare No. 1 Fort Union specimens, includes M<sup>1-2</sup> evidently of *Tetraclaenodon* and closely comparable to *T. symbolicus*, although the variability of this species, lack of adequate material of the upper dentition, and some differences from other specimens, perhaps individual and perhaps of minor taxonomic value, make the reference uncertain.

**TETRACLAENODON cf. PUERCENSIS (Cope, 1881)**

A few fragmentary specimens demonstrate the presence of a larger species of *Tetraclaenodon*. These include a left upper M<sup>2</sup> from the Gidley Quarry (U.S.N.M. no. 9620), associated left dm<sup>4</sup> and M<sup>1</sup> from Loc. 6 (American Museum), associated left M<sup>2</sup> and part of

M<sup>3</sup> from Loc. 82 (American Museum), and specimens figured by Douglass (1902b, p. 222) from Loc. 5 or 6. These specimens vary considerably among themselves, and they are not clearly distinguishable from variants of *T. puercensis*, but they are inadequate for specific determination and do not definitely establish the presence of that species in this field.

The original of Douglass' 1908, pl. 1, fig. 4, is perhaps a right P<sup>3</sup> of this same form, but this is uncertain, and the other isolated teeth referred to *Tetraclaenodon* by Douglass seem still more dubious.

There are also preserved with U.S.N.M. no. 11913 a right and a left M<sup>1</sup> (possibly M<sup>2</sup>) probably of *Tetraclaenodon* and, at least in their worn condition, closely resembling *T. puercensis*. They certainly are not associated with no. 11913, since they are from a much older individual, and it is very improbable that they are of the same species, and not at all clear that they are congeneric. No. 11913 is recorded as from Loc. 11 or 13. These localities are at about the same level and are the highest that have yielded identifiable mammals. A note by Silberling with the specimens seems to leave little doubt that these specimens were derived from that level except in the highly improbable case that they have accidentally been substituted for two other upper molars in the collection.<sup>8</sup> *Tetraclaenodon* has not otherwise been reported from beds as late as this, and these teeth are inadequate to establish its presence although they make it probable.

#### Genus GIDLEYINA Simpson<sup>9</sup>

*Gidleyina* SIMPSON, 1935d, p. 240.

*Type*.—*Gidleyina montanensis* (Gidley).

*Distribution*.—Upper Paleocene, Fort Union, Montana.

*Diagnosis*.—Gidley<sup>10</sup>: "Cheek teeth bunolophodont; first and second upper molars subquadrate, consisting of four principal cusps, two intermediates, and a well-developed mesostyle, conules connected by continuous lophs with the summit of the protocone; premolars 3 and 4 with well-developed protocones, but with metacones rudimentary; thus superficially they each consist of two principal transversely placed cusps."

<sup>8</sup> The teeth themselves are not marked, as are most specimens in the collection.

<sup>9</sup> In one draft of his manuscript Dr. Gidley referred the type of this genus to *Euprogonia*, in another to *Ectocion*, and in a third, presumably the most recent, to *Proectocion*, new genus. His new generic name is, however, preoccupied by *Proectocion* Ameghino, 1904, and therefore it cannot be used. He intended to change it, for he had made a pencil notation, "change name, not related to *Ectocion*, but rather to *Progonodon*", but I find no other name in his notes or on his labels and so have been forced to supply one. It is highly appropriate that the genus should be named for Dr. Gidley. (*Gidleya* Cossman, 1907, is a fossil boid.)

<sup>10</sup> Quoted from what is probably the most recent draft of Dr. Gidley's manuscript, the only one in which a new genus is proposed.



Simpson: Closely resembling *Ectocion*, but upper premolars with much smaller metacones, first and second molars with slightly smaller mesostyles and hypocones, protoconules of  $P^3-4$  and  $M^{1-2}$  slightly more united by lophs to protocone.

*Discussion.*—The molars of this genus can hardly be distinguished generically from *Ectocion*, although unlike any known species in details. The premolars, however, are distinctly less molariform and at once distinguish *Gidleyina* from *Ectocion*. It is well known that from partial dentitions alone it is often difficult or impossible to determine even the ordinal affinities of genera in these ancient faunas, but in this case every indication is that *Gidleyina* is in fact related to *Ectocion*, and perhaps ancestral to it.<sup>11</sup>

If this is correct, it is clear that the *Ectocion* line was already distinct from that of *Phenacodus* in the Middle Paleocene and had already acquired a mesostyle and slightly more lophiodont pattern, although in other respects, such as the complication of the premolars, not more advanced than *Tetraclaenodon*.<sup>12</sup>

Among Torrejon genera, *Gidleyina* most closely resembles *Protoselene* in many respects but is at once distinguished by the large and posterointernal protocone on  $P^3$ , distinct conules on  $P^4$ , and other lesser details, suggesting that the relationship is not very close. The distinctions from *Protoselene* are resemblances to *Ectocion*.

In addition to the type, based on an upper jaw, I tentatively refer two species based on lower jaws to this genus. They are described below.

#### GIDLEYINA MONTANENSIS (Gidley)

#### FIGURE 72

*Gidleyina montanensis* (GIDLEY) Simpson, 1935d, p. 240.

*Type.*—Princeton no. 12048, part of left maxilla with  $P^3-M^2$  and a probably associated right  $P^2$ .

*Horizon and locality.*—Loc. 68, about 1,000 feet above *Gidley Quarry*, Fort Union, Sweetgrass County, Mont.<sup>13</sup>

<sup>11</sup> This is Dr. Gidley's opinion in all three drafts of the manuscript on this form, but still later he noted that affinity is closer with *Protogonodon*. This seems to me highly improbable and was perhaps noted rather as a point to check than as a conclusion.

<sup>12</sup> In one of his manuscripts Dr. Gidley proposed placing the *Tetraclaenodon-Phenacodus* and the *Gidleyina-Ectocion* phyla in different subfamilies. Even if we grant that the phyla were distinct from Middle Paleocene to lower Eocene, they are so similar that considering them as two subfamilies seems to me disproportionate to the classification of other groups of mammals.

<sup>13</sup> There are now no locality data with the specimen. One of Dr. Gidley's manuscripts says "Near sec. 23, R. 15 E., T. 5 N. . . near top of Fort Union No. 2 of Silberling." Localities 4, 52, and 54 are the only ones in (or near) this section—the *Gidley Quarry* and a nearby exposure near the same level. As far as I can determine, no Princeton material came from anywhere near here. Another of Dr. Gidley's drafts, and apparently the latest, says "From the vicinity of Bear Butte. . . . Exact level not known, but probably from near the middle of the section of this locality." Mr. Silberling, however, remembers the discovery of the specimen and positively states that it was found at the locality now numbered 68. Two other specimens perhaps of this species are from the cluster of localities in the western part of T. 5 N., R. 15 E., where most of the Princeton specimens were found, some 1,500 feet above the base of No. 3.

*Diagnosis.*—Gidley<sup>14</sup> “ $P^2$  to  $M^3=31+$  mm;  $M^{1-2}=13.1$  mm; length of  $M^1=6.4$  mm, greatest width=9.1 mm, width across hypocone and metacone=8.3 mm, greatest width of  $M^2=9.8$  mm, other measurements of this tooth same as those of  $M^1$ ; parastyle and mesostyle prominent, mesostyle angular and continuous with the ectoloph;  $P^4$  with uninterrupted internal cingulum, and with low but well-defined lophs connecting the summit of the protocone with the protoconule and base of the metacone respectively.”

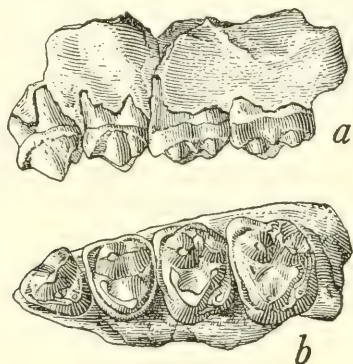


FIGURE 72.—*Gidleyina montanensis* (Gidley), Princeton Univ. no. 12048, left upper jaw: *a*, External view; *b*, crown view. One and one-half times natural size.

*Discussion.*—The  $P^2$  probably associated with the type is a simple 2-rooted tooth with one laterally compressed external cusp, somewhat anterior on the crown, and a small posterointernal expansion of the base but not true protocone.

My measurements of the type are as follows:  $P^4$ – $M^2$ , 19.6;  $M^{1-2}$ , 13.8; length  $P^2$ , 4.5; width  $P^2$ , 3.1; length  $P^3$ , 5.9; width  $P^3$ , 5.8; length  $P^4$ , 5.7; width  $P^4$ , 7.2; length  $M^1$ , 7.0; width  $M^1$ , 9.0; length  $M^2$ , 6.9; width  $M^2$ , 9.9.

Two other specimens from the same cluster of localities all at about the same level are in the Princeton collection. Princeton no. 14195 is an  $M^2$  similar to that of the type but slightly larger and with the hypocone more internal. These could be individual variations. Princeton no. 14190 is an isolated  $P_4$  7.2 mm in length and 4.8 mm in width. Its size is almost exactly that of the corresponding tooth of ?*G. silberlingi*, but the protoconid and metaconid are closer to each other and the metaconid is relatively more posterior.

<sup>14</sup> I quote Dr. Gidley's diagnosis from the draft in which he placed the species in a new genus. His other two diagnoses view it as a species of *Tetractenodon* and of *Ectocion*, respectively, and are therefore inappropriate.

?GIDLEYINA SILBERLINGI (Gidley)<sup>15</sup>

## FIGURE 73

?*Gidleyina silberlingi* (GIDLEY), Simpson, 1935d, p. 240.

*Type*.—U.S.N.M. no. 6166, partial left lower jaw with  $P_3$ – $M_3$ . Collected by A. C. Silberling. (In the same lot are a partial right lower jaw with  $M_{2-3}$  and another right lower jaw fragment with  $M_2$  and the heel of  $M_1$ . They probably belong to the same species but include parts of one or two different individuals and are excluded from the type material.)

*Horizon and locality*.—Loc. 27, about 400 feet above the base of Fort Union No. 3, Wheatland County, Mont.<sup>16</sup>

*Diagnosis*.—Gidley: “. . . About the size of or a little smaller than *E. minor* [= *Tetraclaenodon pliciferus*, G. G. S.] . . . Jaw relatively long and slender, especially anteriorly; the teeth proportionately narrow transversely . . . with a decided tendency to selenodonty . . . The paraconid in the molars is vestigial or wanting, and  $P_4$  is submolariform . . . the heel . . . having the crescentic form of that of the molars, while the metaconid is large and as high as the protoconid.”

*Discussion*.—It is possible that this is the lower dentition of *Gidleyina montanensis*. Since, however, it cannot be demonstrated to belong even to this genus and since among lower dentitions it is a distinctive and interesting type that requires some means of reference until its association with upper teeth can be established, it seems quite proper to accept Dr. Gidley's decision to define it as a species, which can be reduced to synonymy later, if necessary, with no great confusion.

In comparison with other known lower jaws, this is generically distinct from any previously described. *Ectocion* is similar but has a simple longitudinal crest on  $P_3$ , instead of an incipient crescent, while  $P_4$  is more complicated and molariform, with a distinct posterointernal cusp absent in the present specimen. The molars offer no contrast definitely of generic value, unless it be the somewhat larger and more definitely closed trigonid basins and less distinct vestigial paraconids of ?*Gidleyina silberlingi*. The possibility that *Gidleyina* is not really ancestral to *Ectocion* or, on the other hand, that ?*G. silberlingi* does not belong to *Gidleyina* is enhanced by the fact that whereas the upper

<sup>15</sup> In a draft of the manuscript on this family, Dr. Gidley describes this as a species of *Euprotogonia* (= *Tetraclaenodon*). On the specimen label he has crossed out “*Euprotogonia*” and written “*Ectocion*.” It is thus evident that he recognized the probable relationship of this jaw to the new genus I have named *Gidleyina*, since this was also successively identified by Dr. Gidley as *Euprotogonia* and as *Ectocion* before its generic distinction was recognized. I have not quoted his diagnosis in full, giving only enough to validate his claim to authorship of the species, since it was written before he had recognized the genus here named *Gidleyina* and therefore is not fully apropos. My comparisons following the diagnosis suffice for the expression of more fully studied opinion as to diagnosis and affinities.

<sup>16</sup> Given on labels, etc., as “Sweetgrass County”, but, as can be seen on the map, this is one of several localities slightly north of the county line.



teeth of *Gidleyina montanensis* are almost ideally prototypal to those of *Ectocion*, the lower teeth called ?*G. silberlingi* seem to be progressing either more rapidly or in a different direction in the development of  $P_3$  and the molar trigonids. This is not certain, however, as these characters are highly variable and an apparent reversion of this sort is not inconceivable.

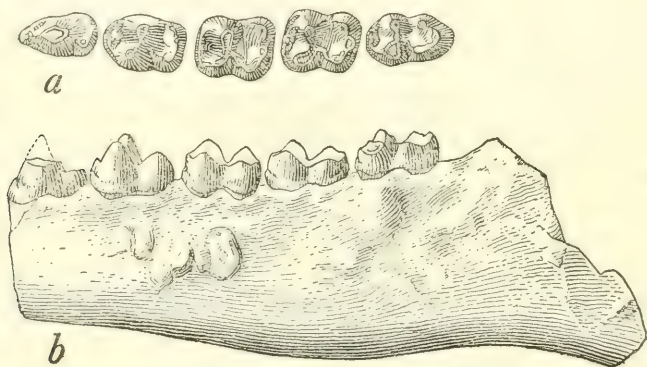


FIGURE 73.—? *Gidleyina silberlingi* (Gidley), U.S.N.M. no. 6166, left lower jaw: a, Crown view; b, external view. One and one-half times natural size.

$P_3$  differs markedly from that of *Tetraclaenodon* in its incipient crescent and basin, but  $P_4$  is basically similar. The molar paraconid is much less distinct in ?*G. silberlingi* than in most specimens of *Tetraclaenodon*, although approached by a few extreme variants of the latter, and the enamel is much less rugose, the crests less crenulated. These characters suggest *Protoselene*, but in the latter even  $P_4$  is much less molariform, with the metaconid strong in ?*G. silberlingi*, barely incipient at best and the talonid very different.

The following measurements are from the type: Length  $P_3$ , 6.7; width  $P_3$ , 3.9; length  $P_4$ , 7.2; width  $P_4$ , 4.7; length  $M_1$ , 7.0; width  $M_1$ , 5.4; length  $M_2$ , 7.3; width  $M_2$ , 5.4; length  $M_3$ , 7.3; width,  $M_3$ , 4.6.

#### ?GIDLEYINA SUPERIOR (Simpson)

##### FIGURE 74

?*Tetraclaenodon superior* SIMPSON, 1935d, p. 239.

*Type*.—U.S.N.M. no. 11913, part of left lower jaw with talonid of  $M_1$ ,  $M_2$ , and  $M_3$  still in capsule. Collected by A. C. Silberling.<sup>17</sup>

*Horizon and locality*.—Loc. 11 or 13, about 3,000 feet above the base of Fort Union No. 3, Sweetgrass County, Mont.

*Diagnosis*.—Lower molars with paraconids vestigial, broad trigonid basins with crenulated anterior margin, crenulations otherwise slight.

<sup>17</sup> The two upper molars apparently of *Tetraclaenodon*, discussed on a previous page, are preserved in the same lot of material but are not associated with the lower jaw and were definitely excluded from the type material of this species.

External cingulum absent, talonids incipiently lophoid. Talonid of  $M_2$  markedly narrower than trigonid. Lower molars of about the size of those of *Tetraclaenodon symbolicus* but slightly narrower relatively. Somewhat longer and distinctly wider than those of ?*G. silberlingi*.  $M_2$  length 7.7, trigonid width 6.2, talonid width 5.5.

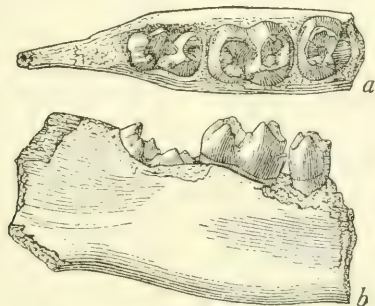


FIGURE 74.—?*Gidleyina superior* (Simpson), U.S.N.M. no. 11913, left lower jaw: a, Crown view; b, internal view. One and one-half times natural size.

*Remarks.*—This distinctive but imperfectly known species was at first referred, with a query, to *Tetraclaenodon*, but with the comment that it might belong to *Gidleyina*. The crucial evidence of the premolars is lacking, but after further study it seems probable that it is congeneric with ?*Gidleyina silberlingi*. The relatively slight enamel crenulation, the structure of the trigonids, and the incipiently lophodont talonids are distinctions from species surely referred to *Tetraclaenodon* and points of resemblance to ?*G. silberlingi*. Reference to *Gidleyina* depends on that of the last-named species, discussed above.

#### Family PERIPTYCHIDAE Cope, 1882

##### Subfamily ANISONCHINAE Osborn and Earle, 1895

Anisonchines are among the commonest fossils in the Puerco and Torrejon, but in the present fauna they are neither abundant nor varied. One form cannot at present be distinguished from the Torrejon species *Anisonchus sectorius*. Only one other form, *Coriphagus montanus*, is recognized. This genus also occurs in the Torrejon, but the species is distinct. The recognition that *Mixoclaenus* is a synonym of *Coriphagus* and that these animals are not oxyclaenids, as generally supposed, but primitive anisonchines clears up a decided taxonomic anomaly and also casts important light on the origin and affinities of the Anisonchinae.

The five genera of this subfamily so far distinguished may be recognized by criteria presented in table 59.

TABLE 59.—Comparison of dentition characters in fine genera of *Anisonchinae*

| Genus                    | P <sub>3</sub>                  | P <sub>4</sub>                                                                                   | M <sub>1-2</sub>                                                                                  | Protostyle and hypocone                                                                                                 | P <sub>3-4</sub>                                                                                                                                      | Paraconids                                                                                              | Heel of M <sub>3</sub>                    |
|--------------------------|---------------------------------|--------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------|-------------------------------------------|
| <i>Coriphagus</i> .....  | With minute protocone rudiment. | With distinct small subconical protocone.                                                        | Markedly transverse, subquadrate, with angulate and emarginate outer borders.                     | No distinct protostyle. Hypocone posterointernal to protocone, developed as point on cingulum nearly enveloping latter. | Elongate, with minute anterior cusps, moderate basined heels.                                                                                         | Distinct, nearly internal.                                                                              | Short, hypoconulid poorly differentiated. |
| <i>Ilaploconus</i> ..... | Without protocone.              | With large crescentic protocone applied to and enveloping the amphilcone.                        | Less transverse, obliquely triangular, rounded outer borders.                                     | Protostyle small. Hypocone strong, posterointernal to protocone.                                                        | Elongate, no anterior cusps, strong basined heels.                                                                                                    | Absent.....                                                                                             | Elongated, hypoconulid a distinct cone.   |
| <i>Anisonchus</i> .....  | With strong protocone.          | With large crescentic protocone, not so closely applied to outer cusp as in <i>Ilaploconus</i> . | Moderately transverse, subquadrate, rounded outer borders.                                        | Protostyle small or absent. Hypocone strong, posterointernal to protocone.                                              | Elongate, large anterior cusps, moderate heels generally basined.                                                                                     | Vestigial but generally distinct, submedian.                                                            | Do.                                       |
| <i>Hemithlacus</i> ..... | do.....                         | With large subconical protocone.                                                                 | Moderately transverse, symmetrical, rounded outer borders.                                        | Small, symmetrically placed, subequal.                                                                                  | Bulbous, small or no anterior cusps, heels small, P <sub>4</sub> generally basined but P <sub>3</sub> generally not.                                  | Vestigial but distinct, submedian.                                                                      | Do.                                       |
| <i>Conacodon</i> .....   | Without protocone.              | do.....                                                                                          | Transversely, obliquely triangular to subquadrate, outer border slightly angulate and emarginate. | Hypocone more internal than posterior to protocone, developed as point on cingulum enveloping latter.                   | Bulbous or elongate, small or no anterior cusps, heels small moderate, that of P <sub>4</sub> basined, that of P <sub>3</sub> basined or not basined. | Distinct on M <sub>1</sub> , small and submedian on M <sub>2</sub> , same or absent on M <sub>3</sub> . | Do.                                       |



Genus *CORIPHAGUS* Douglass

*Coriphagus* DOUGLASS, 1908, p. 17.

*Mixoclaenus* MATTHEW and GRANGER, 1921, p. 7.

*Type*.—*Coriphagus montanus* Douglass.

*Type of Mixoclaenus*.—*Mixoclaenus encinensis* Matthew and Granger.

*Distribution*.—Middle Paleocene, Fort Union, Montana, and Torrejon, New Mexico.

*Diagnosis*.— $P_1$  1-rooted.  $P_{3-4}$  subequal, somewhat swollen but elongate, with minute anterior basal cusps and small heels basined posterointernally. Molars relatively small, trigonids larger than talonids and notably higher, paraconids distinct and nearly internal, trigonids basined with cusps crested, poorly differentiated, and not conical.  $M_3$  much reduced, with hypoconulid distinguishable but not prominent.  $P^3$  with very rudimentary protocone,  $P^4$  with distinct but small subconical protocone,  $M^{1-2}$  transverse, subquadrate, outer borders angulate and emarginate, distinct hypocones postero-internal to protocones and on cingula nearly enveloping the latter.

*Discussion*.—Douglass based this genus and its type species on a single but unusually complete lower jaw with  $P_2$ - $M_3$ , found by Silberling in the Silberling Quarry. In 1913 and 1916 parties under Dr. Granger found three<sup>18</sup> specimens of a similar form in the Torrejon, and in 1921 Matthew and Granger described these as *Mixoclaenus*. They then noted the resemblance of *Mixoclaenus* to *Coriphagus* but cannot have realized, from Douglass' somewhat schematic figure, how close it is. They decided to hold *Mixoclaenus* as distinct at least until discovery of the upper dentition of *Coriphagus*. Matthew's fuller description of *Mixoclaenus* (Pale. Mem.) was written before 1921 (probably in 1917) and was not corrected. It does not mention the resemblance to *Coriphagus*. The upper dentition of *Coriphagus montanus* is now partly known, and it has been possible to compare original specimens of that species and of *Mixoclaenus encinensis*. The conclusion is that the two species are unquestionably congeneric and hence that *Mixoclaenus* is a synonym of *Coriphagus*. They compare very closely in every known part, and the type species of the two supposed genera differ only in size and doubtfully in slight variations of proportions.

Douglass (1908) referred *Coriphagus* to the ?Insectivora, without family assignment. Matthew and Granger (1921) placed "*Mixoclaenus*" in the Oxyclaenidae but noted resemblances to Mioclaeninae and Anisonchinae.<sup>19</sup> In his longer work Matthew (Pale. Mem.) has

<sup>18</sup> Matthew mentions four, describing only two of them, but I can only find three in the collection.

<sup>19</sup> Hay (1930) followed them in placing *Mixoclaenus* (which he wrongly ascribed to the Tiffany) in the Oxyclaenidae, but he placed *Coriphagus* in the Plagiomenidae, a family with which it has practically nothing in common. Schlosser (1923) placed *Mixoclaenus* (which he wrongly ascribed to the Puerco) in the Oxyclaenidae and *Coriphagus* in the Mioclaenidae. These and other casual references are accompanied by no evidence and require no discussion.

outlined the evidence in more detail. (He is discussing *Mixoclaenus*, which now proves to be *Coriphagus*.) The only oxyclaenid character given is "upper molars resembling those of *Chriacus*", but he adds that they are wider transversely, more triangular, external angles more prominent,<sup>20</sup> hypocone less so, and  $M^3$  much reduced and more transverse. With these, and other modifications, the resemblance to *Chriacus* is really quite attenuated. Matthew notes that the rounded condyle and other characters of the jaw and the small premolariform canine are not oxyclaenid but do not approach condylarths or insectivores. I add that they do, almost to identity, approach the Anisonchinae. Matthew also notes, but rejects as inconclusive, some resemblance to *Didelphodus*, leptictids, and *Palaeosinopa* in the molars, but adds that the premolars suggest the Mioclaeninae but are more like the Anisonchinae.

This genus has, in fact, all the diagnostic characters of the Anisonchinae and nothing that decisively indicates pertinence to any other group. The upper and lower premolars are of fully anisonchine type and are especially suggestive of *Conacodon cophater*.<sup>21</sup> They differ in such details, well within the morphological range of the Anisonchinae generally, as the incipient development of a protocone on  $P^3$  and the less transverse  $P^4$ . This last tooth is intermediate between the "round premolar cusp" type (*Hemithlaeus* and *Conacodon*) and the "flat premolar cusp" type (*Haploconus* and *Anisonchus*), adding to the evidence already given by Matthew that these are not, as Osborn and Earle thought, major phyletic divisions of the Anisonchinae. The lower premolars still more closely resemble those of *Conacodon cophater*, the only definite differences being that they are slightly less inflated and have the anterior basal cuspule a little smaller (but larger than in *Conacodon entoconus*). Matthew (Pale. Mem.) mentions the heavy and peculiar wear on these teeth in *Coriphagus* ("*Mixoclaenus*"), truncating them obliquely. This wear occurs in all Anisonchinae and is almost diagnostic of the group.

The molars are on the whole more primitive or generalized than those of other anisonchines, which is what induced Matthew to refer the genus to the Oxyclaenidae. Yet they have the basic anisonchine characters. The upper molars markedly resemble those of *Anisonchus gillianus* and *Conacodon cophater*, apparently the most primitive in this respect among other anisonchines. From the former they differ chiefly in the less rounded outer contour, shorter internal slope, and development of the hypocone on a cingulum around the protocone. The first and last of these characters are resemblances to *Conacodon cophater* in which, however, the internal slope is also long and the hypocone is more internal, with respect to the protocone, than in *Cori-*

<sup>20</sup> This does not seem to me to be quite certain.

<sup>21</sup> *Conacodon entoconus* differs greatly from the smaller species and might almost be distinguished from it generically.

*phagus*.  $M^3$  is markedly reduced and very transverse, a resemblance to *Conacodon cophater* but here somewhat intensified.

In the lower molars the large swollen trigonids with the tips of the cusps pinched together, giving an aspect difficult to describe but characteristic when seen, is diagnostic of Anisonchinae and typically developed in *Coriphagus*. The paraconids are retained and are closely similar to those of *Anisonchus gillianus*, possibly a trifle more internal, but hardly more so than in some specimens of that species; in *A. sectorius* they are more definitely median. The molar talonids are relatively smaller and their cusps less conical and distinct, especially on  $M_3$ . This is perhaps the most aberrant feature of *Coriphagus*, considered as an anisonchine, but the difference from such a form as *Conacodon cophater* is really slight.

The characters of the mandible mentioned or shown by Matthew are almost identical with those of other anisonchines about the same size.

*Coriphagus* is in many respects the most primitive known anisonchine, representing, in view of its age, an unprogressive surviving type. Its closest comparisons are with *Conacodon cophater* and *Anisonchus gillianus*, both Puerco species and older than the known species of *Coriphagus*. *Coriphagus* carries still closer the marked resemblance already noted between the anisonchine and the hyopsodontid dentitions. Were no other anisonchines known, it could very well be classed as a hyopsodontid representing another incipiently divergent line in addition to the several already known in that group. But all these divergent characters are in the direction of the more specialized anisonchines, and these in turn show marked resemblance to the still more specialized periptychines. The whole hyopsodontid-periptychid complex seems to bear the definite stamp of divergence from a common ancestry.

#### CORIPHAGUS MONTANUS Douglass

##### FIGURES 75, 76

*Coriphagus montanus* DOUGLASS, 1908, p. 17.

*Type*.—Carnegie Mus. no. 1669, left lower jaw with  $P_2$ – $M_3$ . Collected by A. C. Silberling.

*Horizon and locality*.—Type from Silberling Quarry, several referred specimens from Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

*Diagnosis*.—Smaller than *C. encinensis* (see measurements). Lower teeth relatively narrow.  $M_3$  less reduced relative to other teeth.

*Discussion*.—The differences in proportions given are not entirely certain, since they depend on only one specimen of *C. encinensis*, and these characters are variable. The size difference is slight and in itself might not warrant full specific status, but its constant association with different provenience makes it certainly significant. Every di-



mension of all three specimens of *C. encinensis* is larger than the corresponding dimension of any of the seven available specimens of *C. montanus*. The best single comparison is of the length of  $M_1$ , which compares as follows, by Fisher's formula:

$$\begin{array}{l} LM_1, C. montanus: N\ 6, M\ 3.25 \\ LM_1, C. encinensis: N\ 2, M\ 3.70 \end{array} \left\{ \begin{array}{l} d\ 0.45, t\ 4.39, P < 0.01. \end{array} \right.$$

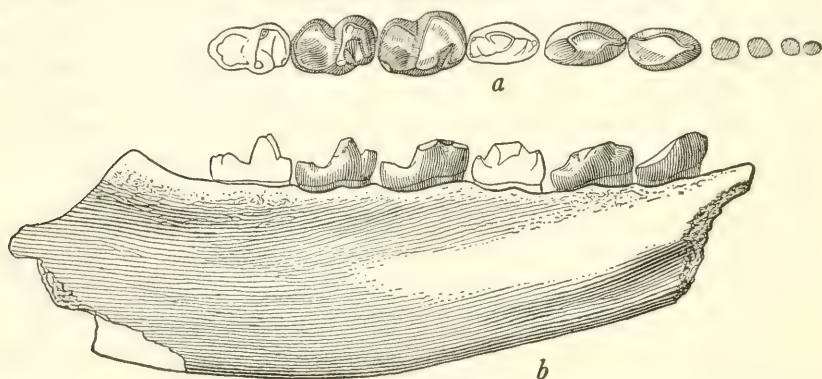


FIGURE 75.—*Coriphagus montanus* Douglass, U.S.N.M. no. 9334, with parts in outline supplied from U.S.N.M. nos. 9599 and 9685, left lower jaw: *a*, Crown view; *b*, internal view. Four times natural size.

The difference is certainly significant although not great.<sup>22</sup>

Table 60 gives ranges and means for the National Museum specimens of *C. montanus* and corresponding dimensions of the paratype of *C. encinensis*, Amer. Mus. no. 17074. The material is not sufficiently abundant for the calculation of other statistical constants.

TABLE 60.—Numerical data on lower dentition of *Coriphagus montanus* and *C. encinensis*

| Dimension               | <i>C. montanus</i> |         |      | <i>C. encinensis</i><br>(Paratype) |
|-------------------------|--------------------|---------|------|------------------------------------|
|                         | N                  | R       | M    |                                    |
| LP <sub>3</sub> -----   | 3                  | 2.7-2.8 | 2.77 | 3.2                                |
| WP <sub>3</sub> -----   | 3                  | 1.4-1.7 | 1.53 | 2.1                                |
| LP <sub>4</sub> -----   | 2                  | 2.3-2.5 | 2.40 | 3.1                                |
| WP <sub>4</sub> -----   | 2                  | 1.4-1.6 | 1.50 | 2.3                                |
| LM <sub>1</sub> -----   | 6                  | 3.1-3.5 | 3.25 | 3.7                                |
| WM <sub>1</sub> -----   | 6                  | 2.1-2.2 | 2.13 | 2.8                                |
| LM <sub>2</sub> -----   | 6                  | 2.5-2.9 | 2.72 | 3.4                                |
| WM <sub>2</sub> -----   | 6                  | 2.0-2.4 | 2.18 | 2.8                                |
| LM <sub>3</sub> -----   | 3                  | 2.3-2.8 | 2.60 | 2.9                                |
| WM <sub>3</sub> -----   | 3                  | 1.7-1.9 | 1.80 | 2.2                                |
| LM <sub>1-3</sub> ----- | 2                  | 8.2-8.7 | 8.45 | 9.9                                |

<sup>22</sup> The mean of *C. encinensis* is only 14 percent greater than for *C. montanus*, and it is to be stressed that this is not in itself and stated in this way of specific value. The largest specimen of *C. montanus* is 13 percent greater than the smallest, and the paratype of *C. encinensis* is only 6 percent larger than the largest of our specimens of *C. montanus* in this dimension. With large series the two species would doubtless intergrade in size, yet they are certainly distinct.

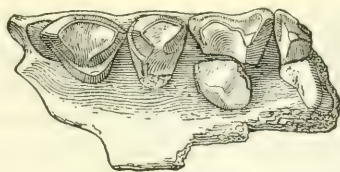


FIGURE 76.—*Coriphagus montanus* Douglass, U.S.N.M. no. 9591, left upper jaw, crown view. Four times natural size.

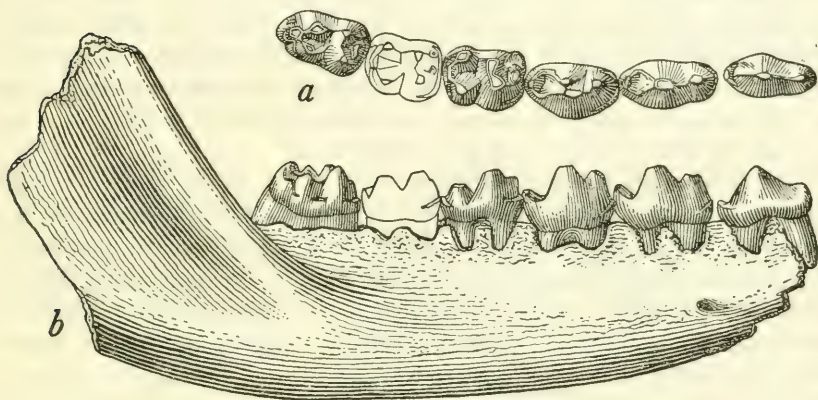


FIGURE 77.—*Anisonchus sectorius* (Cope), referred specimen from the Lebo, U.S.N.M. no. 9267, right lower jaw: *a*, Crown view; *b*, external view. Twice natural size.

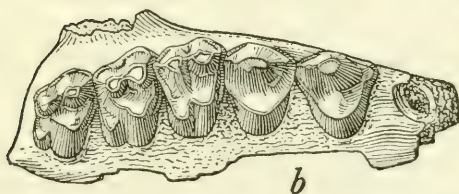
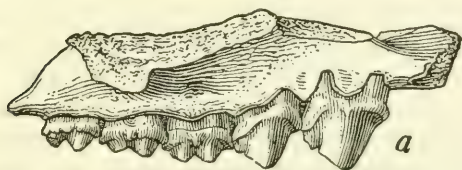


FIGURE 78.—*Anisonchus sectorius* (Cope), referred specimen from the Lebo, U.S.N.M. no. 9263, right upper jaw: *a*, External view; *b*, crown view. Twice natural size.

U.S.N.M. no. 9591 is a left upper jaw with  $P^2$ - $M^1$  and about half of  $M^2$ , from the Gidley Quarry, which is certainly referable to *Coriphagus montanus*. It is deeply worn but well shows the generic characters.  $P^3$  may be slightly less transverse and the external cingulum of  $P^4$  weaker than in *C. encinensis*, and all the teeth are slightly smaller, but the agreement in structure is very close.

Genus *ANISONCHUS* Cope, 1881

*ANISONCHUS SECTORIUS* (Cope, 1881)

FIGURES 77-79

Douglass (1902b, p. 222) described and figured an *Anisonchus* that he compared with *A. sectorius* but mentioned the possibility that it might be distinct. The National Museum collection includes a series of excellent specimens of this genus, and their pertinence to *Anisonchus sectorius* can be rather positively established, although they may well pertain to local races as will be pointed out.<sup>23</sup>

*Anisonchus* is the only genus represented by good material in this fauna that seems to be represented here by the same species as that occurring in the Torrejon. It therefore is a special point of attack for considering the relationships of these two widely separated Middle Paleocene deposits, and the material has been subjected to detailed and lengthy analysis. The results are not entirely conclusive, largely owing to the small size of the available pure samples, but they nevertheless are of considerable interest, and they also provide data that must be useful in future work. The full analysis would fill many pages with numerical and morphological data and calculations, and so it is not published here *in extenso*, but only such figures as are most necessary to illustrate the general conclusions reached.

A study was first made of the Torrejon specimens themselves to see whether more than one species or race could be distinguished, particular attention being paid to possible distinction between material from the two principal fossil levels of the Torrejon. The results of this analysis were negative: From the data at hand it is not possible to subdivide the Torrejon material, all of which is referable to *Anisonchus sectorius*.<sup>24</sup> Despite considerable variation, there is only one specimen, Amer. Mus. no. 3533, that stands out as strongly aberrant. It was collected by Baldwin in 1885, and the exact horizon and locality are not recorded. Even this specimen, however, is so close to typical *A. sectorius* that it would be methodologically incorrect to discard it from the general sample.

<sup>23</sup> Labels show that Dr. Gidley referred some of the Fort Union specimens to *Anisonchus sectorius* and some to a new species, but he left no diagnosis or discussion. I have carefully endeavored to visualize his concept of the new species, thinking that it might correspond with one of the inconclusively indicated local races, but this does not seem to be the case, and I am unable to ascertain the characters relied on by him.

<sup>24</sup> It may be noted, however, that Matthew is incorrect in believing one of the cotypes of *A. mandibularis* to belong to *Anisonchus sectorius*. Whatever the position of this very dubious species, it is not a synonym of *A. sectorius* and probably does not belong in *Anisonchus*.

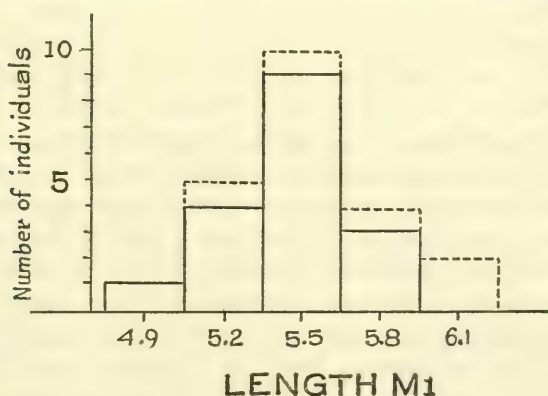


The general statistical data on the simple dimensions of the lower teeth of all Torrejon specimens of *Anisonchus sectorius* in the American Museum are presented in table 61.

TABLE 61.—Numerical data on lower dentition of *Anisonchus sectorius*

| Variate               | N  | R       | M         | $\sigma$  | V        |
|-----------------------|----|---------|-----------|-----------|----------|
| LP <sub>3</sub> ----- | 8  | 5.8-6.8 | 6.28±0.11 | 0.30±0.08 | 4.8±1.2  |
| WP <sub>3</sub> ----- | 8  | 2.8-4.1 | 3.22±0.14 | 0.40±0.10 | 12.3±3.1 |
| LP <sub>4</sub> ----- | 17 | 5.3-6.6 | 5.86±0.07 | 0.30±0.05 | 5.2±0.9  |
| WP <sub>4</sub> ----- | 17 | 3.5-4.3 | 3.88±0.05 | 0.22±0.04 | 5.7±1.0  |
| LM <sub>1</sub> ----- | 17 | 5.0-5.8 | 5.47±0.05 | 0.22±0.04 | 5.7±1.0  |
| WM <sub>1</sub> ----- | 17 | 3.5-4.2 | 3.87±0.04 | 0.17±0.03 | 4.5±0.8  |
| LM <sub>2</sub> ----- | 21 | 4.8-5.6 | 5.34±0.04 | 0.20±0.03 | 3.8±0.6  |
| WM <sub>2</sub> ----- | 23 | 3.7-4.4 | 4.06±0.03 | 0.17±0.02 | 4.1±0.6  |
| LM <sub>3</sub> ----- | 14 | 5.1-6.1 | 5.58±0.08 | 0.28±0.05 | 5.0±1.0  |
| WM <sub>3</sub> ----- | 14 | 3.2-4.0 | 3.54±0.05 | 0.20±0.04 | 5.7±1.1  |

The lower dentition material from the Crazy Mountain Field now available consists of three specimens from the Gidley Quarry, three from Loc. 25, four from Loc. 51, and one each from Locs. 50 and 18. The highest number of comparable specimens from a single horizon and locality is only three, for P<sub>4</sub> from the Gidley Quarry.

FIGURE 79.—Histogram of the length of M<sub>1</sub> in *Anisonchus sectorius* (Cope): In solid outline, Torrejon specimens (American Museum); in dotted outline, Lebo specimens (National Museum).

By inspection of the specimens and of their dimensions, it is suggested that there is local differentiation. Thus in the series from the Gidley Quarry, Loc. 25, and Loc. 51, each local sample seems to be reasonably homogeneous and to differ slightly from that of the other two localities. In the jaws from the Gidley Quarry the lower molars are longer, but not noticeably wider, than those from Loc. 25. The very poor material from Loc. 51 suggests closer agreement with the Gidley Quarry at least in P<sub>4</sub> and M<sub>1</sub>, but two isolated M<sub>3</sub>'s from there

are closer to those from Loc. 25. This impression of slight heterogeneity cannot now be considered dependable or formally recognized. The differences could hardly be of more than subspecific scope in any event and perhaps are merely those of separate strains within one subspecies, and the data are too few to establish them as real.

The best data for material from one locality, dimensions of  $P_4$  and  $M_1$  from the Gidley Quarry, may be compared with the Torrejon sample by Fisher's t-test, previously mentioned, with the following results:

| VARIATE | $N_1 + N_2$ | t    | P            |
|---------|-------------|------|--------------|
| $LP_4$  | 20          | 2.22 | $<0.05>0.02$ |
| $WP_4$  | 20          | 1.60 | $<0.2>0.1$   |
| $LM_1$  | 19          | 2.83 | $<0.02>0.01$ |
| $WM_1$  | 19          | 1.74 | $<0.2>0.1$   |

Thus these two teeth are probably significantly longer, but not wider, than those of the Torrejon sample as a whole. Since the latter is heterogeneous in origin and perhaps as to race, it does not necessarily follow that the Gidley Quarry race does not occur in the Torrejon, but it probably does not. Comparison of the whole Fort Union sample, however, shows no significant difference, as the following figures for the only variates probably significant in the Gidley Quarry sample show:

| VARIATE | $N_1 + N_2$ | t    | P           |
|---------|-------------|------|-------------|
| $LP_4$  | 25          | 1.95 | $<0.1>0.05$ |
| $LM_1$  | 22          | 1.66 | $<0.2>0.1$  |

In short, the evidence now is that the Fort Union sample may include more than one local or temporal genetic group of minor scope and the same may be true of the Torrejon material. At least one of these minor groups in the Fort Union is distinct from the Torrejon sample as a whole and probably from any group included in the latter. But the definitive separation of these minor groups cannot be accomplished from the data now available, and there is no significant difference between the Fort Union *Anisonechus* as a whole and that of the Torrejon as a whole. All are referable to a single species, *A. sectorius*.

TABLE 62.—Numerical data on  $P_4$  of *Anisonechus sectorius*

| Variate      | N  | R         | M                 | $\sigma$          | V               |
|--------------|----|-----------|-------------------|-------------------|-----------------|
| $LP_4$ ----- | 25 | 5. 3-6. 6 | 5. 94 $\pm$ 0. 05 | 0. 31 $\pm$ 0. 04 | 5. 2 $\pm$ 0. 7 |
| $WP_4$ ----- | 25 | 3. 5-4. 3 | 3. 92 $\pm$ 0. 04 | 0. 20 $\pm$ 0. 03 | 5. 2 $\pm$ 0. 7 |

As an indication of the variation of the whole species as thus known, data for  $P_4$ , a rather variable and characteristic tooth best represented in the combined collections, are here presented (table 62). Individual measurements of the many specimens studied, and many other data, are on hand and will be permanently filed.

The uniformity of these results with those based on Torrejon specimens only is striking. Despite the great increase (one and a half times) in the size of the sample by the addition of specimens of widely different provenience, the two means are increased by only 0.08 and 0.04, respectively, the first figure only 0.01 more than the corresponding standard error for the smaller sample and the second less than the corresponding standard error. The standard deviations are altered by amounts considerably less than their standard errors in the smaller sample and the same is true of one coefficient of variation, while the other is not changed at all.

The interest of the coefficients of variation for the Torrejon sample should also be pointed out. One of them, for  $WP_3$  is unusually high, but this is largely caused by the single aberrant or abnormal specimen previously mentioned.<sup>25</sup> If we accept  $P_3$  as abnormally variable or as represented by some extraneous material, the other eight coefficients of variation range from 3.8 to 5.7 and average 4.8.<sup>26</sup> The accumulation of such figures is of great importance in view of our almost complete lack of any exact knowledge of the variability of fossil species in samples collected under the usual field conditions.

The preceding discussion is based on lower teeth. The upper dentitions have also all been examined and compared, but they merely substantiate the evidence of the lower dentitions, and the samples are less satisfactory in all respects.

## Order PANTODONTA Cope, 1873 (as suborder), new usage

The order Dinocerata (emended from Dinocerea) was proposed for the Uintatheres by Marsh in 1872. In 1873 Cope proposed to reduce this to subordinal rank and with the new suborder Pantodonta, for the coryphodonts, placed it in the order Proboscidea. In 1875 the two suborders were transferred by Cope to a new order Amblypoda. In 1883 he added to this order the suborder Taligrada, based solely on *Pantolambda*, and in 1897, as stated on an earlier page, added the periptychids to the Taligrada. Marsh in 1884 proposed "Amblydactyla" and "Coryphodontia" as strict synonyms of Cope's names (which Marsh claimed to be essentially preoccupied) Amblypoda and

<sup>25</sup> Omission of this specimen would reduce  $V$  from 12.3 to  $7.5 \pm 2.0$ .

<sup>26</sup> This is within twice the standard error (that is, within the range of probable true values) for all the single coefficients and is within less than the standard error for all but two. If the aberrant individual be omitted, it is also well within the range of probable true values for  $P_3$ .



Pantodonta, respectively, but these names have not been generally accepted.

The classification thus achieved is well summed up by Osborn (1898):

Order AMBLYPODA:

Suborder Taligrada:

Periptychidae.

Pantolambdidae.

Suborder Pantodonta:

Coryphodontidae.

Suborder Dinocerata:

Bathyopsidae.

Uintatheriidae.

This arrangement is now classic and with slight modifications has since come into all but universal use. Nevertheless, in the light of later discovery and research, it has little to recommend it.

The probable affinities of the periptychids with the condylarths, rather than with the pantolambdids, have been discussed on a previous page. On the other hand, all recent work (see especially Simpson, 1929d, and Patterson, 1934) tends to emphasize the essential unity of *Pantolambda* and *Coryphodon* and their respective allies. The known pantolambdids are not ancestral to the known coryphodonts, and family separation is warranted, but they are so similar in structure aside from primitive or progressive features generally correlated with greater or lesser age that there seems no reason to place them in separate suborders, and the distinction between Taligrada and Pantodonta is unwarranted.

The uintatheres, on the contrary (Simpson, 1929d and elsewhere), seem to be a group independent of the pantolambdids and coryphodonts from a very remote time and linked to them only through a prot- or perhaps even pre-ungulate, non-"amblypod" ancestry. The classic arrangement was undoubtedly influenced by the belief that taligrades, pantodonts, and dinoceratans represented offshoots of a single stock appearing successively in time with correspondingly progressive specializations. Now it is clear that this simple picture does not correspond to the facts. Among the supposed "taligrade" periptychids the more advanced members are the only ones that show any considerable resemblance to the pantolambdids in foot structure, but they cannot possibly be ancestral to the latter not only because they are contemporaneous but also because aside from the feet (and in part including them) their structure is very different. The idea of successive offshoots does apply to the pantolambdids and coryphodonts, but it decidedly breaks down again with the coryphodonts and uintatheres because these groups are not successive but contemporary phyla, and it is the latest and most advanced members of each that show some resemblance, which hence is only convergent, and the earlier members are even more decisively dissimilar.

The classification seems, in fact, to have been based on grades of foot specialization, over the prototypal ungulate foot, rather than on characters peculiar to natural phyla. It thus united periptychids and pantolambdids because they had advanced relatively little in limb structure, even though their phyletic relations must have been distant. It separated (subordinally) pantolambdids and coryphodonts because the former were less and the latter more advanced in limb specilization, despite the clear evidence that these groups are closely related phyletically. And finally it united coryphodonts and uintatheres because both have specialized limb structures, but overlooked their marked phyletic separation.

The revision of nomenclature for the accurate representation of these newer points of view is difficult. The following diagram shows the relationships of the classic names to the groupings now considered natural:

|                   |                                                 |               |                |                 |                                            |  |
|-------------------|-------------------------------------------------|---------------|----------------|-----------------|--------------------------------------------|--|
| Condylarthra..... |                                                 |               |                |                 |                                            |  |
| Amblypoda.....    |                                                 |               |                |                 |                                            |  |
| Taligrada.....    |                                                 |               |                |                 |                                            |  |
| Pantodonta.....   |                                                 |               |                |                 |                                            |  |
| Dinocerata.....   |                                                 |               |                |                 |                                            |  |
| Condylarthra..... |                                                 |               |                |                 |                                            |  |
| Amblypoda.....    |                                                 |               |                |                 |                                            |  |
| Taligrada.....    |                                                 |               |                |                 |                                            |  |
| Pantodonta.....   |                                                 |               |                |                 |                                            |  |
| Dinocerata.....   |                                                 |               |                |                 |                                            |  |
| Condylarthra..... |                                                 |               |                |                 |                                            |  |
| Pantodonta.....   |                                                 |               |                |                 |                                            |  |
| Dinocerata.....   |                                                 |               |                |                 |                                            |  |
|                   | (Various other families,<br>see "Condylarthra") | Periptychidae | Pantolambdidae | Coryphodontidae | Uintatheriidae (including<br>Bathyopsidae) |  |

Since both periptychines ("Catathlaeus") and anisonchines (*Anisonchus*) were explicitly cited among the genera belonging to the Condylarthra when that group was first proposed, since most definitions of Condylarthra need little or no alteration to include the periptychids, and since no other ordinal or subordinal name has been based primarily on the periptychids, the removal of the Periptychidae to the Condylarthra raises no nomenclatural problem.

The name *Dinocerata* was originally based on the uinatheres alone and has always been taken as referring to them and including only them,<sup>27</sup> so there can be no question as to the propriety of continuing this name in this usage.

What remains is to settle on a name for the *Pantolambdidae* and *Coryphodontidae*. Some students (including me, 1931) have used "*Amblypoda*" essentially in this sense, usually including the *Peripitychidae*. There is good precedent for such a restriction of a name to one of several groups formerly included in it, and it is generally more advisable than coining a new name. In the present case, however, it should be avoided if possible. "*Amblypoda*" was based about equally on the coryphodonts and the uinatheres. To exclude the uinatheres from it is not quite the removal of the type group but certainly is a radical change in usage and one not well justified.

The name "*Taligrada*" might be expanded to this usage, but this also is objectionable. As originally defined it was carefully drawn so as to exclude and contrast with the best-known members of the group for which a name is now sought, that is, the coryphodonts. Furthermore, in the past 40 years it has almost invariably been taken to include or even to be typified by the *peripitychids*.

"*Pantodonta*" has none of these objections. It was proposed and has always been used for typical members of the group now in question. No animals foreign to this group have ever been called *pantodonts*. Its original definition, although brief, offers a good contrast with both *Condylarthra* and *Dinocerata*, even as those groups are now understood, and would include the *pantolambdids* (not known when the name was proposed), so that we are using the name exactly in the sense of the original author, in fact more so than he did later. The fact that a group that he later excluded from the *Pantodonta* is now included seems to be of no particular importance, especially as his original conception is not thereby changed. It is entirely proper in taxonomy to extend a name formerly applied to one group to include another later found to be closely related and is open to much less question than would be the exclusion from a named group of a subdivision on which it was originally largely based (as in excluding uinatheres from the *Amblypoda*). The name "*Amblypoda*" I would discard altogether, as not pertaining to any group acceptable as natural or convenient in modern taxonomy.

The present conception of the group *Pantodonta* may be summarized as follows:

---

<sup>27</sup> Marsh did suggest synonymy with Cope's broader "*Amblypoda*", but in fact nothing but the uinatheres was meant to be included in the original description and Marsh later (1884) accepted this restriction, for he proposed "*Amblydactyla*" to replace "*Amblypoda*" and to include both coryphodonts and uinatheres, with only the latter listed as "*Dinocerata*."



Order PANTODONTA: A group of middle-sized to large, very archaic ungulates (or "subungulates"). The dentition is little or not reduced in number, and remains practically brachyodont, but exhibits a high degree of lophiodonty even in the earliest members. The primitive pattern is strongly selenodont but this is secondarily masked to some extent in later forms. The canines are apparently always large, and may develop into great tusks. Skull and jaws are generally massive with very powerful muscle attachments. The brain remains very small and primitive. The limbs are massive and strong, ambulatory to graviportal, and retain many primitive features such as separate radius and ulna, tibia and fibula, and five toes on each foot. Carpus and tarsus retain and strongly accentuate the alternating arrangement.

Family Pantolambdidae: Relatively less advanced forms, with the teeth fully selenodont, the skull roof little or not flattened, the tail long and heavy, and other primitive characters.

Subfamily Pantolambdinae: Lighter, more ambulatory types of smaller size and with astragalus still retaining some condylarth characters. Middle Paleocene. North America.

Subfamily Barylambdinae: Heavy graviportal types of larger size, with fully specialized pantodont type of astragalus. Upper Paleocene. North America.

Family Coryphodontidae: Highly specialized forms, large in size, all with graviportal limbs, teeth with primitive crescents considerably modified, skull roof broad and flat, tail reduced. Upper Paleocene—lower Eocene in North America. Lower Eocene in Europe. Upper Eocene to Middle Oligocene in Mongolia.

Family Pantolambdodontidae: A somewhat dubious group known from lower jaws only, which suggest relationship with *Pantolambda* but have numerous differences in details. Upper Eocene. Mongolia.

The present fauna contains few remains of pantodonts, but *Pantolambda* is represented by various fragmentary specimens, some of which indicate a species first defined, and at present known only, from this fauna.<sup>28</sup>

## Family PANTOLAMBDIDAE Cope, 1853

### Genus PANTOLAMBDA Cope, 1883

Douglass (1902b, p. 224) described and figured an upper premolar perhaps of this genus. It is about the size of  $P^2$  of *P. bathmodon*, but differs somewhat in form, the main cusp being more central and the external margin less sharply notched. The National Museum materials does not serve to define this form. The second *Pantolambda* mentioned by Douglass (1908, p. 24) probably belongs to the species defined below.

<sup>28</sup> The present conception of the Pantodonta, especially as regards its essential unity as here defined, owes much to Patterson's discovery of complete skeletons of *Barylambda* and to his fine studies of them (Patterson, 1933, 1934, 1935, 1937). Although not from the Crazy Mountain Field, the type species and specimen of *Titanoides* was found in the Fort Union and named and described by Gidley (1917), and it was originally proposed to include a discussion of it in this work, but Patterson's studies make this quite unnecessary.

## PANTOLAMBDA INTERMEDIUS Simpson

## FIGURE 80

*Pantolambda intermedius* SIMPSON, 1935d, p. 244.

*Type*.—U.S.N.M. No. 8384. Left lower jaw with  $M_{1-2}$  and alveoli of C-P<sub>4</sub>, associated with symphysis fragment with right  $I_{1-2}$  and alveoli of left  $I_{1-3}$ . Collected by Dr. J. W. Gidley.

*Horizon and locality*.—Gidley Quarry, Fort Union, Middle Paleocene horizon, Crazy Mountain Field, Mont.

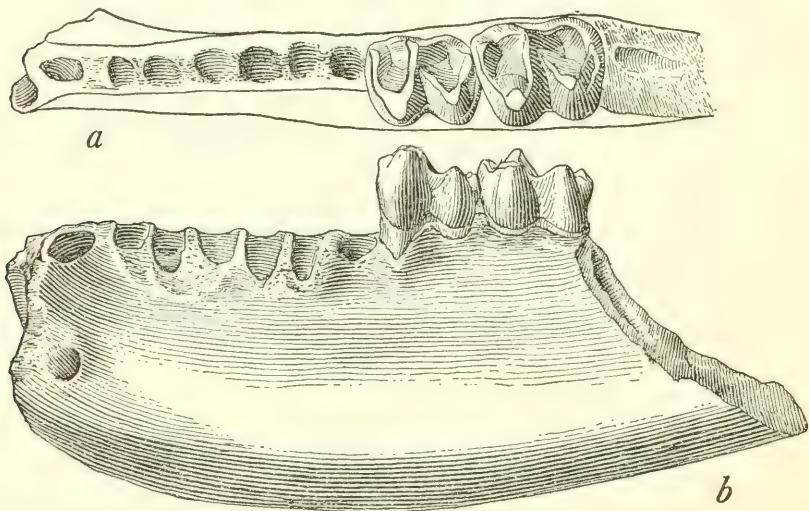


FIGURE 80.—*Pantolambda intermedius* Simpson, U.S.N.M. no. 8384, right lower jaw: *a*, Crown view; *b*, external view. Natural size.

*Diagnosis*.—Intermediate in size between *P. bathmodon* and *P. cavirictus*.  $P_1$  with one large root, close to canine, followed by short diastema.  $P_{2-4}$  2-rooted. Lower molars closely resembling those of *P. cavirictus* but entoconid more distinct.

*Discussion*.—The type has  $M_{1-2}$  somewhat corroded on the inner side. An isolated lower premolar, probably  $P_2$ , no. 9598, from the same quarry as the type, is probably of this species. It is 2-rooted (as was  $P_2$  of the type) and is as long as  $P_2$  of *P. cavirictus* but is considerably narrower and simpler. In *P. cavirictus* the posterointernal crest from the main apex bifurcates and a sharp branch runs from it anterointernally, whereas in this tooth the posterointernal descending crest is less prominent throughout and has no bifurcation or antero-internal branch. The talonid is a narrow, simple heel.

On the whole this species seems to resemble *P. cavirictus* but is both smaller and more primitive structurally. Length  $M_1$ , 13.2;

width  $M_1$ , 11.2; length  $M_2$ , 14.8; width  $M_2$ , 12.1; length  $P_2$  (referred) 11.8; width  $P_2$  (referred), 6.8. (The widths may have been a little greater before the teeth were corroded.)

PANTOLAMBDA or allied genera, species undetermined

U.S.N.M. no. 6155 is an isolated  $M^2$  from "¼ mile N. of Fish Creek Creek 200 ft. E. of Melville and Harlowton Road", in Fort Union No. 3. This almost certainly means Loc. 28; it is about a half mile from Fish Creek, but no other mammal locality more nearly corresponds with the indication. This horizon is 400 feet above the base of No. 3 and about 550 feet above the Gidley Quarry. This tooth resembles the smaller Torrejon specimens referred to *P. cavirictus* but has the cingula, external and internal, better developed.

No. 9858, from Loc. 18, well up in Fort Union No. 3, is a fragment of an upper molar probably of the same species as no. 6155.

No. 9694, from Loc. 54, the same level as the Gidley Quarry, is a symphysis and isolated  $M_2$ , which also approach small *P. cavirictus* in size and is perhaps of this same species, although possibly still smaller. It is nearer *P. cavirictus* than *P. intermedius* in size.

No. 10048, from the Gidley Quarry, closely resembles a lower posterior premolar of *Pantolambda bathmodon* in form but is smaller, 7.3 mm long and 5.9 wide.

All these specimens are inadequate for determination, but they show that pantolambdids were not uncommon in this general area and that they were varied, despite the fact that conditions did not lead to the good preservation of their remains.

There are also isolated bones, without associated teeth, from the horizon of the Gidley Quarry and in one unimportant case, the base of No. 3, which probably belong to *Pantolambda*. All are as large as the corresponding parts of Torrejon *P. cavirictus* and differ only in insignificant details. Since the probabilities suggest that some of these belong to *P. intermedius*, it may be that the latter was a small-headed form, with body equal to *P. cavirictus* in size but jaws and teeth considerably smaller. In the absence of associated material, however, this is obviously hypothetical.



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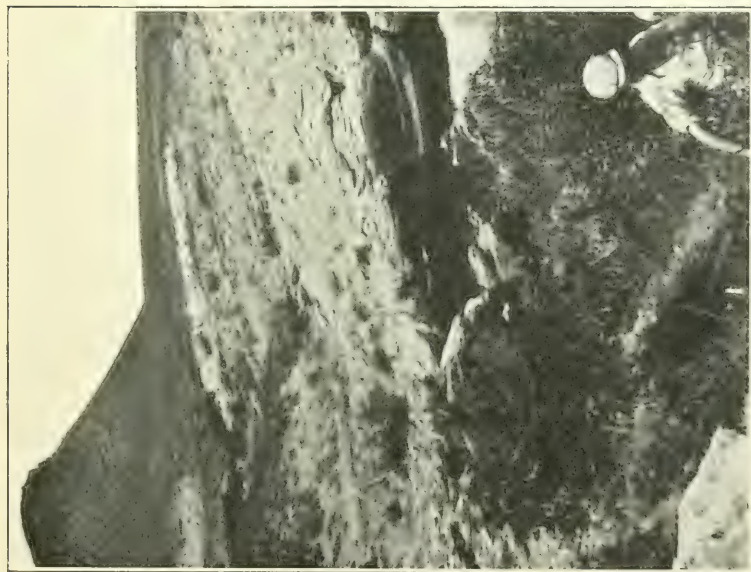
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# BEAR AND LEBO FORMATIONS, CRAZY MOUNTAIN FIELD, MONT.

- 1, Sec. 26, T. 6 N., R. 16 E., looking approximately west near south line of section. The alternating pale sandstones and shales in foreground are upper part of the Bear, and the bench across upper part of the picture is approximately on the Bear-Lebo contact. The hill in left foreground is formed by the Lower Lebo, or Fort Union No. 1, and is capped by a resistant somber sandstone typical of that division. Loc. 65, the lowest at which mammals have been found in this field, is near the base of this hill immediately to the left (south) of the area covered by the photograph.
- 2, Lower Lebo (Fort Union No. 1) sandstone in Sec. 35, T. 6 N., R. 15 E., near Loc. 9.



FORT UNION GROUP, CRAZY MOUNTAIN FIELD, MONT.

FOR EXPLANATION OF PLATE SEE OPPOSITE PAGE.

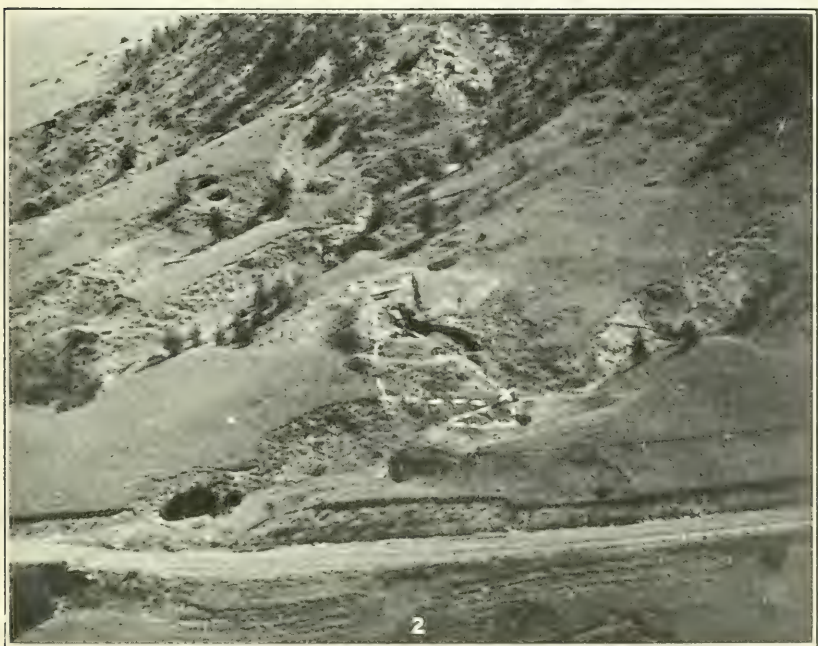


### PLATE 3

- 1, Air view, looking approximately south, with Sec. 33, T. 6 N., R. 16 E., near the middle of the picture (prominent but small isolated timber butte in this section). The meandering watercourse is Widdecombe Creek and is developed on the nonresistant Upper Lebo (Fort Union No. 2), as are the other low sodded areas through the central part of the picture. The main timbered ridge across the photograph is the northwest side of Bear Butte. The broken area between the small outlying butte and the patch of timber (on Bear Butte) farthest to the left, just beyond the road, is Loc. 5, one of Douglass' two localities where mammals were first found in the Fort Union. Part of Lion Butte forms the skyline in the center and right parts of the picture.
- 2, Air view of the east side of the north end of Bear Butte, looking approximately south in Sec. 34, T. 6 N., R. 16 E. The rimrock of Bear Butte, along the upper edge of the picture, is the basal Melville (No. 3) sandstone, and the rest of this area is all on the Upper Lebo (No. 2). The shale exposure in the coulee above the road in the upper left of the picture is Loc. 6, one of Douglass' discovery sites.

PLATE 4

- 1, Air view of the Gidley Quarry and vicinity, looking slightly north of east, the foreground in Sec. 23, T. 5 N., R. 15 E. The slope in the foreground, on which the quarry is visible, is on the Upper Lebo (No. 2), as is also the broad valley of the Widdecombe Creek in the upper left. The higher level in the upper and right parts of the picture, and along the horizon, is supported by the basal Melville (Fort Union No. 3) sandstone. It is typically marked by evergreen timber, but in the foreground this timber extends sparsely well down onto the Lebo, but only on talus derived from the Melville. Bear Butte is dimly visible along the left part of the horizon, and a small corner of Lion Butte is seen in the upper right corner. Between these, small hills upheld by isolated patches of the Melville may be seen.
- 2, Air view of the Gidley Quarry, a closer view, looking more to the north, of part of the foreground of fig. 1. The picture was taken in 1935 and shows an advanced stage in the American Museum quarrying operations. The approximate area covered by the U. S. National Museum work (and since filled in) is indicated by dotted lines. The larger section (A of Silberling's notes) is on the far (north) side of the small coulee, and the smaller (B) on the near side. The original discovery was made in the coulee near the spot marked by the cross.



FORT UNION GROUP, CRAZY MOUNTAIN FIELD, MONT.

FOR EXPLANATION OF PLATE SEE OPPOSITE PAGE.





FORT UNION GROUP, CRAZY MOUNTAIN FIELD, MONT.

FOR EXPLANATION OF PLATE SEE OPPOSITE PAGE.

PLATE 5

- 1, Air view, looking approximately west-northwest, the foreground in Sec. 4, T. 5 N., R. 16 E. The small drainage basin in the foreground is on the Upper Lebo (Fort Union No. 2). The Silberling Quarry is in the upper part of the main right (northwest) branch of the coulee. The sparse timber marks the basal Melville (No. 3) sandstone and the top of Bear Butte, which here, near the middle of its length, is at its narrowest point. Beyond this is the valley of Widecombe Creek, hidden by Bear Butte, and beyond this, dim in the photograph, rise low hills, without timber, developed on the Lower Lebo (No. 1) along the axis of the Widecombe Creek anticline.
- 2, Site of the Silberling Quarry, looking approximately north in Sec. 4, T. 5 N., R. 16 E. The two figures near the middle of the picture stand near the ends of the main section of the quarry. The slope is on the uppermost part of the Lebo (upper No. 2), but the basal Melville (No. 3) lies immediately above, and numerous talus blocks from it are seen. The quarry is not discernible as such, since the picture was taken in 1932, 24 years after intensive work there.

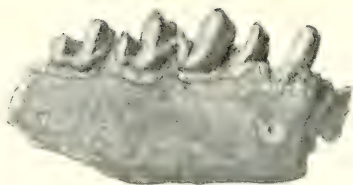
PLATE 6

- 1, Typical exposure of the Lower Melville sandstone, looking approximately north in Sec. 23, T. 5 N., R. 15 E. The valley in the upper right corner is on the Upper Lebo (No. 2), with low barren hills of the Lower Lebo (No. 1) beyond it.
- 2, Shell limestone in the Melville at Loc. 40, Sec. 29, T. 5 N., R. 15 E. Such beds characterize the middle part of the Melville, although the formation is predominantly of sandstone and shale. The invertebrate beds are generally not so thick or so well exposed as they are at this locality. The apparent nodules are gastropod shells.





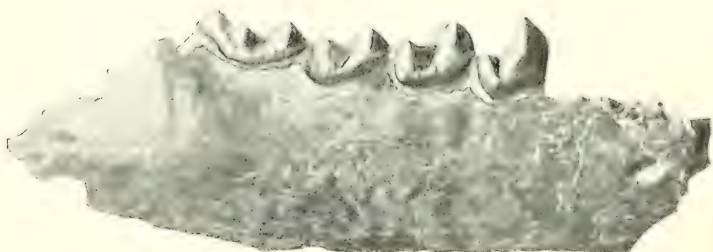
MELVILLE FORMATION, CRAZY MOUNTAIN FIELD, MONT.  
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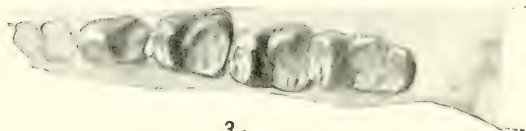
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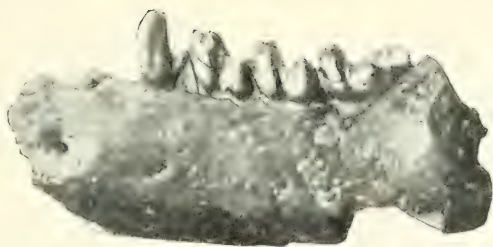
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## FORT UNION PRIMATES.

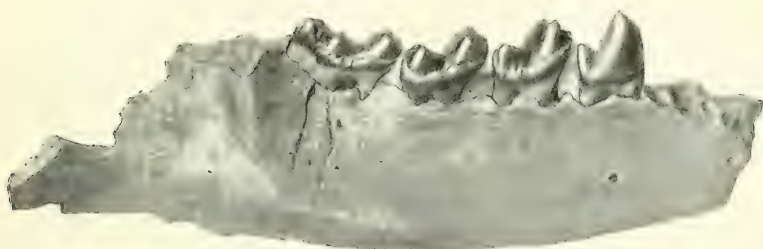
- 1, *Palaeochthon alticuspis* Gidley, part of right lower jaw with  $P_2-M_2$ , type (U.S.N.M. no. 9532), external view, Gidley Quarry; 2, *Paromomys maturus* Gidley, part of right lower jaw with  $P_4-M_3$ , paratype (U.S.N.M. no. 9545), external view, Gidley Quarry; 2a, same, crown view; 3, *P. maturus*, part of right lower jaw with  $P_1-M_1$ , type (U.S.N.M. no. 9473), external view, Gidley Quarry; 3a, same, crown view. (All figures about four times natural size; after Gidley.)



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## FORT UNION PRIMATES.

1, *Pronothodectes matthewi* Gidley, part of left lower jaw with  $P_4-M_3$ , paratype (U.S.N.M. no. 9531), external view, Gidley Quarry; 2, *Paromomys maurus* Gidley, part of right lower jaw with  $P_4-M_3$ , paratype (U.S.N.M. no. 9475), external view, Gidley Quarry; 2a, same, crown view; 3, *P. maurus*, part of left lower jaw with  $P_4-M_3$ , paratype (U.S.N.M. no. 9337), external view, Gidley Quarry. (All figures about four times natural size; after Gidley.)





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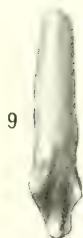
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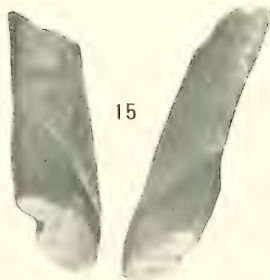
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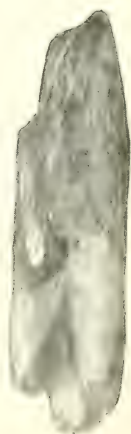
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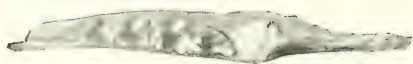
FORT UNION PRIMATES.

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PLATE 9

- 1, *Plesiadapis gidleyi* (Matthew), left upper molar, U.S.N.M. no. 10765, crown view. From the Tiffany beds near Ignacio, Colo.; for comparison with *Pronothodectes*.
- 2, *Pronothodectes matthewi* Gidley, right P<sup>4</sup>-M<sup>2</sup>, type (U.S.N.M. no. 9547), crown view. Gidley Quarry.
- 3, *Plesiadapis gidleyi* (Matthew), right P<sup>1</sup>, U.S.N.M. no. 10659, crown view. From the Tiffany beds near Ignacio, Colo.; for comparison with *Pronothodectes*.
- 4, *Plesiadapis rex* (Gidley), left lower molar, type (U.S.N.M. no. 9828), crown view. Gidley Quarry.
- 5, *Palaeochthon alticuspis* Gidley, right M<sup>1-3</sup>, paratype (U.S.N.M. no. 9550), crown view. Gidley Quarry.
- 6, *Palaeochthon alticuspis* Gidley, right M<sup>1-2</sup>, paratype (U.S.N.M. no. 9551), crown view. Gidley Quarry.
- 7, *Paromomys depressidens* Gidley, right P<sup>4</sup>-M<sup>3</sup>, type (U.S.N.M. no. 9546), crown view. Gidley Quarry.
- 8, Undetermined, probably primate upper incisor, U.S.N.M. no. 10090, lingual view. Gidley Quarry.
- 9, Undetermined, probably primate upper incisor, U.S.N.M. no. 10010, lingual view. Gidley Quarry.
- 10, Undetermined, probably primate upper incisor, U.S.N.M. no. 9928, lingual view. Gidley Quarry.
- 11, Probably *Pronothodectes matthewi* Gidley, upper incisor, U.S.N.M. no. 10005, lingual view. Gidley Quarry.
- 12, Probably *Pronothodectes matthewi* Gidley, upper incisor, U.S.N.M. no. 10044, lingual view. Gidley Quarry.
- 13, Undetermined lower incisor, possibly *Plesiadapis rex*, U.S.N.M. no. 9827, lateral view. Probably Loc. 13.
- 14, Undetermined, possibly multituberculate lower incisor, U.S.N.M. no. 9552, lateral view. Gidley Quarry.
- 15, Undetermined, pair of upper incisors, U.S.N.M. no. 9917, lingual view. Gidley Quarry.
- 16, *Plesiadapis gidleyi* (Matthew), poorly preserved upper incisor, U.S.N.M. no. 10639, lingual view. From Tiffany beds, 5½ miles east of Bayfield, Colo.

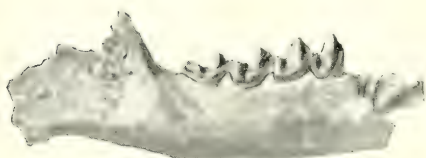
(All figures about four times natural size; after Gidley.)



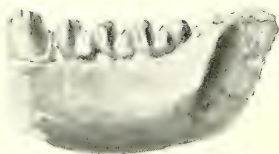
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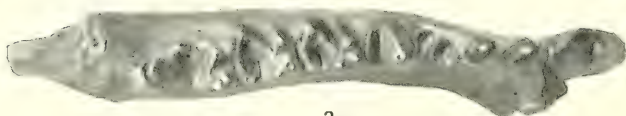
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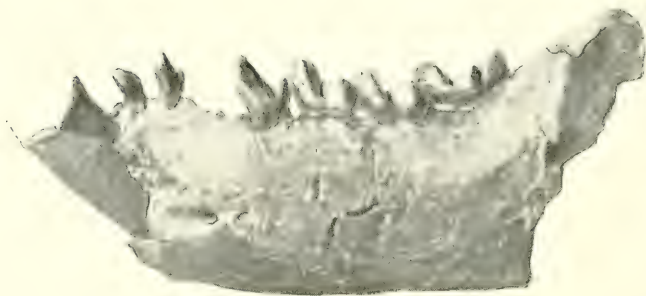
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## FORT UNION PRIMATES.

- 1, *Palenochtha minor* (Gidley), part of right lower jaw with  $P_4-M_3$ , type (U.S.N.M. no. 9639), external view; 1a, same, crown view; 2, *Elphidotarsius florenceae* (Gidley), part of left lower jaw with  $P_4-M_3$ , type (U.S.N.M. no. 9411), external view; 2a, same, crown view; 3, *Pronothodectes matthewi* (Gidley), part of left lower jaw with base of incisor, canine (?),  $P_2$  and  $P_4-M_3$ , U.S.N.M. no. 9332, external view; 3a, same, crown view. (All figures about four times natural size; after Gidley. All from Gidley Quarry.)







# INDEX

(Principal references are given in **boldface**)

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 absarokae, *Didelphodus*, 110.  
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